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SEMI NATURAL VEGETATION AND THE BIOTIC FACTOR

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D Sc. 1934

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I N T R O D U C T I O N

INTRODUCTORY

The object of this work is threefold. In the first place it is intended as a general and descriptive account of typical areas of semi-natural vegetation in Great Britain. Secondly a study of the effect of biotic factors which produce this type of vegetation is involved, and special attention is given to a particular aspect of the biotic factor, i.e. the mechanical aspect. This latter influence has received little attention up to the present. Thirdly the economic applications of the study are investigated

It is obvious that the term semi-natural applies to vegetation which occupies a mid-way position between the natural and the artificial or cultivated. On the one hand natural vegetation consists of areas in a comparatively stable condition, such as heaths and forests, moorlands or salt marshes. These areas appear, through an equilibrium of the factors affecting them, to have reached a climax or a state of sufficient stability to merit their classification as definite associations. Such communities as these have received, and are still receiving, considerable attention from ecologists and a large amount of investigation of the factors affecting them, mainly edaphic and climatic, is being conducted.

Artificial or cultivated vegetation on the other hand is represented by plantations, orchards, arable fields under crops or market gardens and certain types of grass land. The formation of these artificial communities may be effected in the course of a few weeks in the length of time taken to plough up and cultivate a natural area. Such communities are now almost completely under the control of man, and the problems concerning them are mainly of an agricultural nature.

Semi-natural vegetation occupies the intermediate position and while on first consideration its status may appear insignificant it will, upon further thought, be found to be of considerable and increasing importance, particularly in a highly civilised state.

The communities which constitute semi-natural vegetation are those of footpaths, waysides, hedgerows, gateways, waste land and certain types of grass land. Increasing human activity in the form of urbanisation of the countryside, the developement of roads, and means of communication, makes it essential that this type of vegetation should have the status which it merits in an ecological survey of the country.

The factors which produce this type of vegetation are essentially biotic though it is a particular aspect of the biotic factor, i.e. mechanical influence, which is responsible in the main. This influence, which cannot receive the status of a separate factor, has received little, if any, consideration up to the present, and research references are scarce though cursory observations are sometimes recorded. A study of these influences has scientific importance as well as far reaching economic applications.

It is very notable that almost all studies of vegetation in this country and certainly all vegetation problems related to agriculture have been approached from the chemical or edaphic standpoint. The explanation lies in the fact that the earliest investigators were chemists, and their outlook has been acquired by the student, the investigator and the agriculturist. It is hoped to show in the following work that the solution to many ecological problems, especially those of semi-natural vegetation, is to be found by a consideration of some purely mechanical force, and that the edaphic factor does not always exert the influence attributed to it.

Semi-natural vegetation is never in a state of equilibrium, but is essentially dynamic. It has been pointed out that natural associations owe their existence and stability to an equilibrium of the factors concerned. Any mechanical disturbance is bound to upset this balance, and by a shuffling and re adjustment of the factors produce complete change in the vegetation.

The results of the investigations have been exploited economically, in several directions. For example it is found that on the poorest grassland (from the graziers' point of view), that the footpaths traversing it, possess an entirely different flora of species with a high feeding value. A complete understanding of the factors producing this contrast enables the same changes to be produced in the field as a whole. Again in the sphere of weed control, where mechanical agents are responsible for the presence or the propagation of certain weeds, a knowledge of these agents, and their mechanism, is shown to solve the problem of prevention and control.

The influence of domesticated and wild animals upon vegetation is also shown to be due frequently to a mechanical rather than a chemical influence.

In the study of ecology no universal terminology or technique has yet been devised, and there are several shades of opinion as to the applicability of statistical methods. It is for this reason that a whole section o this work (Section 1.) has been devoted to a consideration of the present position, and the policy adopted in the subsequent investigations.

From the purely statistical point of view the data may leave much to be desired, It is hoped they will fully serve their purpose.

SECTION

1

DEFINITIONS AND TECHNIQUE

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Ecology is a comparatively new science, and is not yet an exact one. No universal vocabulary has been adopted, and while the terminology and technique of the leading workers in this sphere all possess much in common, they also vary considerably in many important aspects. There are those who consider that the very nature of the study renders exact measurement impossible, and prohibits the development of ecology beyond the status of a descriptive science. On the other hand several leading workers, most notably Braun-Blanquet, have attempted to devise definite standards of measurement.

Statistical methods, where applicable, are always to be preferred, but in many instances the complexity of the communities under investigation and the peculiar nature of the problems render anything but pure description impossible.

With statistical methods there is a grave danger of becoming deeply involved in a mass of data, obtained at the expenditure of considerable time, which possesses no relevant value and does not assist in the problem under consideration. On the other hand, the collection of data and the intensive study and survey of an area may serve to bring details to notice which might have escaped observation and which may provide the key to the solution of the problem.

Description may often be the resort in certain cases, and may be greatly assisted by photography. Illustration of a phenomenon by means of a photograph provides concrete evidence.

The drawback to qualitative methods is the human factor as there is always a tendency for an investigator to exaggerate any point of particular interest to himself and to observe more readily any phenomonon which goes to prove his own theory.

It appears necessary to adopt a middle course, quantitative methods being avoided when they serve no useful purpose but carried out whenever of value. Description should always be checked as far as possible by statistics and measurement of the factors concerned.

The peculiar nature of certain problems renders it impossible to abide by any fixed technique, but the investigator has to modify orthodox methods or evolve new ones to suit his convenience.

Definitions of Plant Communities.

The definitions approved by the British Empire Vegetation Committee are those now adopted by most ecologists in the description of the units of a plant community. These are quoted below.

"A Plant Community may be defined as any naturally growing collection of plants which, for the purposes of the study of vegetation, can be usefully treated as an entity." Another description is, "A plant community is any collection of plants growing together which have as a whole a certain individuality."

The different types of plant community are as follows :-

(1) The Plant Association. "The association is the largest unit which consists of a definite assemblage of species (usually with definite dominants) and a definite habitat, e.g. the beech oak forest of Central and Western Europe, the spruce pine forest of Northern Europe, the grama buffalo (Bouteloa - Bulbilis) short grass plains of the semi arid regions of North America, the Rhizophora Bruguiera mangrove swamps of many tropical coasts, etc, etc. The association (and also the other units or types of community) is characterised in four main ways; first by a more or less definite floristic composition, secondly by the life forms of its members, especially its dominant members, thirdly by its structure, and fourthly by its habitat, primarily climate, but sometimes by other factors within the region of a given climate."

(2) The Consociation. "The dominant species of an association may occur mingled together, or separated into pure dominant stands which have in other respects the characters of the association. Thus the reed-swamp association in the northern hemisphere often shows pure dominant stands of the genera Scirpus, Typha and Phragmites. In other places these may be mingled together. The communities dominated by single dominants are called consociations, thus the bulrush, the reedmace (sometimes also called bulrush) and the common reed consociations of the reed swamp."

"The consociation is named by the stem of the generic name of the dominant species with the suffix-etum, thus a consociation of Calluna is known as a Callunetum."

The Society. "Within an association or consociation subordinate species (i.e. species which are not association dominants) often form communities of lower rank. They become dominants in certain areas even to the exclusion of the association dominants---- societies then are determined by the local dominance of certain species, other than the association dominants, within an association."

The Clan. Small aggregations of single subordinate species, derived from gregarious growth, either vegetative or by scatterings of seeds over a limited area are conveniently called clans.

Ecotones are transitional belts between well marked communities.

Successional Series. (Seres).

It is essential to draw broad distinctions between the types of plant communities which are in a stable condition and have reached a climax, and those which are in an unstable condition or sub climax. These developmental units are referred to as seres. To the units occurring in a developmental state the suffix - es, is applied thus, associes, consocies, socies, in place of the terms association, consociation and society. A clan in the developmental stage is referred to as a colony.

A sere beginning on bare ground is known as a prisere, whilst a sere appearing where former units have been destroyed is a subsere.

Priseres may be named according to their habitat thus hydrosere and xerosere, psammosere or lithosere.

All the above definitions are in certain cases arbitrary. In the following investigation where the correct definitions are not obvious the reasons for choosing the definitions used are fully discussed.

Floristic Composition of Communities.

The floristic composition of a community, of any type of vegetation, is a list of the species occurring within the particular area.

The listing of the species may be further elaborated by describing the "life form","growth form","vegetation form" or "habitat form" of the individual species.

The distribution and arrangement of the species may be described by their abundance, frequence, dominance, constance, exclusiveness.

To these characters * Braun-Blanquet adds the analytical characters density, sociability, vitality, periodicity, stratification; and the synthetic characters presence (a relative expression of constancy) and fidelity (or exclusiveness).

Definition of Floristic Characters.

Life Form.

"This is the name given to the type of plant body associated with its life history." Raunkiaers system of life forms is the one most commonly adopted. "It is mainly based on the position in regard to the soil surface of the perennating buds which continue the growth of the plant from season to season."

Life form is primarily hereditary, but it may be modified by conditions, e.g. in the following investigations

* An exposition of these characters is given in "Pflanzensoziologie", but Braun-Blanquet ascribes their conception to other workers.

the life form of certain plants is altered by treading. These are then known as "ecads."

* Raunkiaer's system is as follows :-

I. Phanerophytes (bud shoots aerial).

(1) Herbaceous phanerophytes.

(2) Evergreen megaphanerophytes (above 30 m) without bud scales.

(3) " meso " (8-30 m) " "

(4) " micro " (2-8 m) " "

(5) " nano " (below 2 m) " "

(6) Epiphytic phanerophytes.

(7) Evergreen megaphanerophytes with bud scales.

(8) " meso " " " "

(9) " micro " " " "

(10) " nano " " " "

(11) Phanerophytes with succulent stem.

(12) Deciduous megaphanerophytes with bud scales.

(13) " meso " " " "

(14) " micro " " " "

(15) " nano " " " "

II. Chamaephytes (bud shoots protected by snow or fallen leaves).

(16) Suffrutescent chamaephytes, e.g. many Labiatae

(17) Passive decumbent " e.g. spp Sedum saxifraga

(18) Active chamaephytes e.g. Limnaea Empetrum

(19) Cushion plants e.g. Agorilla Raoulia

III. Hemicryptophytes (bud shoots at the soil level).

(20) Protohemicryptophytes

A. Plants without creeping offshoots, Linaria, Verbena, Medicago.

B. Plants with creeping offshoots stolons or rhizomes Urtica, Saponaria.

* This rehresents the system as described by Clements. There are numerous descrihtions and modifications. The system has been elaborated by Braun-Blanquet, who includes the cryhtogams.

(21) Sub rosette plants.

A. Plants without creeping offshoots, Caltha, Geum.

B. Plants with creeping offshoots Ranunculus reptans.

(22) Rosette plants.

A. Plants without offshoots, Primula, Taraxacum, Carex.

B. Plants with offshoots Hieracium, Petasites.

Plants with monopodial rosette.

I. Monopodium with leaves but no scales.

A. Aerial leaf and flower shoots Trifolium pratense.

B. Aerial shoots flower bearing only.

a. Without creeping offshoots. Plantago major.

b. With creeping offshoots. Fragaria, Trifolium repens

II. Monopodium with both leaves and scales.

A. Without creeping offshoots Anemone hepatica.

B. With creeping offshoots Convallaria majalis.

III. Monapodium with scales alone Sedum roseum, (Scop)

IV. Cryptophytes (bud shoots buried in the soil). Geophytes.

(23) Rhizome geophytes Polygonatum.

(24) Timber " Cyclamen.

(25) Tuberous root " Orchis.

(26) Bulb geophytes. Allium. Lilium.

(27) Root bud geophytes. Cirsium arvense. Moneses.

(28) Helophytes. Typha, Scirpus, Equisetum, Sagittaria.

(29) Hydrophytes, Nymphaea, Zostera, Hippuris, Potamogeton.

V. Therophytes (Annuals) Galium aparine, Thlaspi arvense.

A Synusia is a unit of plants of similar life form.

Physiologically dry	B	(3) Oxylophytes (acid soil).
		(4) Psychrophytes (cold soil).
		(5) Halophytes (saline soil).
Physically dry.	C	(6) Lithophytes (rocks)
		(7) Psammophytes (sand and gravel).
		(8) Chersophytes (Waste land)
Climate dry.	D	(9) Erythmophhytes.
		(10) Psilophytes.
		(11) Sclerophytous formation (bush and forest).
Soil physiologically and physically dry	E.	(12) Coniferous formations forest.
Soils favouring mesophytous formation.	F	(13) Mesophytes.

An Ecad is produced by direct and demonstrable adaption to habitat. It is a habitat form in the making.

Modification of Warming's Habitat-form system.

Hydrophytes	I	(1) Emophytes	Submerged.
		(2) Plotophytes	Floating.
		(3) Helophytes.	Amphibious.
Mesophytes.	II	(4) Heliophytes	Sun plants.
		(5) Sciaphytes.	Shade plants.

A. Soil Physiologically Dry.

Xerophytes.	(6) Halophytes	Salt.
	(7) Psycrophytes	Cold.
	(8) Oxyphytes	Lack of oxygen.

B. Soil Physically Dry.

(9) Lithophytes.	Rock.
(10) Psammophytes	Gravel.
(11) Chrysophytes	Rock sub-stratum.

C. Climate Dry ∴ Soil Dry.

(12) Enymophytes	Desert.
(13) Psilophytes	Grass land.
(14) Drymophytes	Scrub.

Terms Describing Distribution and Arrangement.

Quantitative Terms.

Abundance is a term describing the relative numbers of the species in a community.

Frequency expresses the dispersal of the species throughout the community.

Dominance concerns the extent occupied by or covered by the individual of each species. Where several strata of vegetation are present in the community it is necessary to evaluate the dominance of each species separately.

Braun-Blanquet has devised the expression Density, i.e. the ratio between the number (n) of individuals of the same species observed on a certain surface and the

Methods of Evaluating Quantitative Terms.

Abundance.

Braun-Blanquet describes degrees of abundance by figures from 1-5, e.g. (1) Very Rare, (2) Rare, (3) Infrequent, (4) Abundant, (5) Very abundant. This method is not adopted in this work as the information is more suited to large communities and leads to confusion with the term "frequence."

The method applied in these investigations consists in throwing a quadrat at random about the community to be examined, and the recording of the number of such species within the quadrat. The relative abundance of such species is expressed as a percentage of the whole.

The size of the quadrat must be adapted to the particular community. When the species are large, a large quadrat is necessary, and on the other hand, in a grassland community where individuals are small, a small quadrat is utilised.

The great difficulty in assessing abundance of certain species is due to the fact that it is almost impossible to distinguish individuals, (in fact entirely so where time is a limiting factor in carrying out the analysis).

For grassland communities the "percentage tiller-method"has been devised. A 6" x 6" quadrat is cast at random over the community. Series of ten casts are made, and the total number of individuals of each species, judged on the basis of their green living shoots, counted within each quadrat, are fractionated in relation to each other to a total of 10. The taking of ten casts in a series thus allows expression by percentages .

Owing to the extremely laborious nature of the work one series only is taken, in many cases.

The percentage abundance method has great limitations in grass land where, as already stated, it is almost impossible to define individuals and a species possessing a large number of tillers assumes a greater importance than it really merits. In certain parts of this work the estimation of abundance is omitted and in others the method best adapted to the occasion is the one used. The fact that all the estimations are carried out by the writer eliminates any differences which might arise from the comparison of the figures of different individual workers, whose idea of what constitutes an individual plant may vary.

All methods of assessing abundance are open to criticism, but are still better than pure description. The accompanying quantitative estimation, i.e. of frequency and dominance have a qualifying effect upon any statements with regard to abundance, and thus tend to neutralise misconceptions.

<u>Frequency.</u>

This term is often used loosely and should only be used to express dispersal. One method which fails in this respect is that of expressing frequency by literal symbols e.g. l = local, a = abundant, d = dominant, cd = co-dominant, f = frequent, r = rare, sd = sub-dominant, o = occasional. Numerical values are applied to the symbols as follows. r = 1, o = 2, f = 3, a = 4, sd = 4, d = 5, cd = 5. This method is a confusing one and not a true expression of frequency, being confused with dominance and abundance.

The percentage method of estimating frequence is the best for present purposes. A quadrat of convenient size is cast about the area and the incidence of each species coming within the instrument is noted. The quadrat must be of convenient size and adapted to the community. The number of quadrat areas in which a species is noted is expressed as a percentage of the total quadrat areas, thus giving the percentage frequence of the species.

Degrees of frequency can be expressed in categories and a numerical value assigned to each. Thus, if desired, graphical representation may be made.

Dominance.

The expression of dominance is that of relative area covered by the species. In the case of a stratified community each stratum must be assessed separately. An exact method of assessing dominance is not known, and only broad distinctions can be drawn with any degree of accuracy. Even in grass land communities a certain amount of stratification exists.

One method adopted is to assign numerical values to degrees of dominance instead of using the percentage method, e.g.

1 = Covering very feeble.
2 = Species covering from 1/20 to 1/4 of the area.
3 = " " " 1/4 " 1/2 " " "
4 = " " " 1/2 " 3/4 " " "
5 = " " more than 3/4 " " "

A method has been devised for estimating abundance and dominance volumetrically, but this is adapted to the study of areas of considerable extent. The scale used for this method is as follows :-

+ = When the number of individuals and the area covered are both very small.

1 = When the number of individuals is rather large but the area covered is small.

2 = When individuals are very numerous and the area covered is at least 1/20 of the surface.

3 = Any number of individuals covering from 1/4 to 1/2 of the area.

4 = Any number of individuals covering from 1/2 to 3/4 of the area.

5 = Any number of individuals covering more than 3/4 of the area.

* A method of estimating dominance employed in parts of this work is the determination of the relative area occupied by the species, and expression on a percentage basis. This method is best suited to those communities where stratification is negligible.

Density.

The method of estimating density, $D = \frac{n}{s}$, has been described. This is not adopted for general use, practical difficulties being encountered, but it has a certain use to describe belt transects, giving the ratio between the number of individuals of the same species observed on a certain surface and the extent of the surface, in the case of the zones which are dominated by one species.

It will be seen that quantitative methods demonstrate the difficulties of applying mathematics and statistical methods to problems of plant ecology, but though each of the above systems may be weak in itself,

* This more exact method is practicable upon the small areas studied, but not on extensive areas.

by adopting several in combination, a very fair representation of the facts is obtained.

Methods of Expressing Qualitative Terms.

Qualitative terms augment the quantitative by depicting more comprehensively the state of affairs within the community. The former are regarded by Braun-Blanquet as of primary importance compared with the latter.

Constancy or Presence. This may be expressed in categories according to the degree of constance or presence, the following is the method adopted by Braun-Blanquet, a numerical value being assigned to each class:-

5 = Species present in 4/5 to 5/5 of examples or representatives of the association studied.

4 = ------------------3/5 to 4/5----------------

3 = ------------------2/5 to 3/5----------------

2 = ------------------1/5 to 2/5----------------

1 = ---------------in less than 1/5-------------

Constancy is a synthetic conception which rests entirely on the idea of the example of the association.

Constancy is expressed in this work on a percentage basis, e.g. the number of examples in which the species occurs out of 100.

Exclusiveness or Fidelity.

*Five degrees of exclusiveness are distinguished by Braun-Blanquet.

Characteristics.

5 = Exclusive, species almost or quite confined to a given comunity.

* N.B. The use of these degrees in Tables II. VII & XI. Secs 3.4.& 5. refers to the particular community under consideration.

4 = Selective, species found especially in a given community but also, though rarely, found in others.

3 = Preferential, species preferring one given community to others, though growing more or less abundantly in these.

Companions. 2 = Indifferent, species growing more or less abundantly in many diverse communities.

Accidentals. 1 = Strangers, these are species accidentally introduced into any given community.

Sociability. To express the manner in which the individuals of the same species are disposed in relation to one another, five degrees of sociability are arranged, and expressed by numbers.

1 = Shoots growing singly.

2 = In small groups.

3 = In large groups.

4 = In small colonies.

5 = In pure populations.

If individual shoots are densely crowded, the number of sociability may be accompanied by a continuous line (_____), but if more or less separated by a broken line (-----).

"Normal Dispersion" occurs when individuals are distributed according to the calculation of probability.

"Sub-Normal Dispersion" occurs when plants are regularly or artificially distributed as in an orchard.

A plant population becomes more homogeneous as :-

(1) The distribution of individuals of each species is more regular.

(2) The sociability of each species is more uniform.

(3) The density of the species in the population is less unequal between themselves.

Vitality. This is expressed by symbols.

● = Well developed, complete cycle regularly accomplished.

⊙ = Cycle usually incomplete, vigorous vegetative development.

⊖ = Cycle incomplete restricted vegetative development.

○ = Germinating accidentally, not multiplying.

Periodicity. This is described by the words vernal, aestival, autumnal and winter, or in abbrevated form v, ae, au, w.

Stratification. The method of describing this character is as follows :-

(1) Tree Stratum.

(2) Shrub Stratum.

(3) Herbaceous Stratum.

(4) Ground or Moss Stratum.

Methods of Charting Vegetation.

Large Scale Surveys. These are carried out by ordinary survey methods, employing the usual instruments. Ordnance survey maps may be shaded coloured or marked with symbols to denote the communities and their units, which have been surveyed.

Small Scale Surveys. Small communities may be surveyed and mapped, the units of the community being denoted by colouring shading or symbols. The latter, in the form or letters or marks, may express the conditions present to a minute degree as individual plants may be indicated, and the size of the letter or mark may denote the relative size of the plant.

Quadrat Charts. A given area enclosed within a quadrat of suitable dimensions may be supplied in detail. If the quadrat be permanently marked, subsequent maps will provide a record of succession.

Line Charts. This method may substitute the above. A line may be drawn by means of a cord or wire and the incident species charted. If the points be made permanent (e.g. wire staples on posts) subsequent charts may be made over the identical line of the previous one.

Belt Transects. This method consists of the mapping of a belt of convenient width (from a few cms to several metres according to the community) with symbols or letters indicating individual species. Many modified forms of transects are used.

Line Transects. By this method a line is drawn between two points and the incident species are mapped. It is possible to show the relative distance occupied by the species.

Bisects. A bisect is produced by cutting a trench through a community and mapping the root and shoot system.

Profile Charts. These charts show the vegetation and its stratification in profile but do not include the root system.

Habitat Conditions.

Habitat is the product of certain influencing factors, though the plants which compose it may indirectly effect the habitat by influencing these factors.

The factors may be defined as climatic, edaphic (the chemical and physical influence of the soil) and biotic (the influence of animals), the physiographic factor is largely a climatic factor as physiography produces local climate. Habitat may be defined as "the sum total of the conditions of the environment which are effective in determining the existence of an association on a given area."

The factors affecting the habitat are to a certain extent interrelated.

Climatic Factors. Light is a very potent climatic factor as will be illustrated in subsequent sections of this work.

Temperature, in its various degrees, exerts a great influence on the habitat. Air temperature and soil temperature are equally important. Soil temperature is not influenced by air temperature to the extent supposed. Hours of sunlight greatly influence soil temperature by irradiation, this may be demonstrated by correlating daily fluctuation in soil temperature with hours of sunshine recorded. Aspect and colour, organic matter and water content also influence the temperature of the soil.

The influence of rainfall upon vegetation is too obvious to require elaboration.

Humidity and evaporating power of the air are accounted as of greater importance than rainfall owing to their effect on transpiration.

Wind and exposure exert an influence by stunting vegetation. There are a number of plants which are structurally adapted to wind exposure.

Edaphic Factors. The soil exerts a great influence in vegetation as is realised by all agriculturists though it may be demonstrated in this work that the influence is often exaggerated, and that phenomena ascribed to the edaphic factor may be due to some other cause.

The most important considerations in regard to the soil is its physical structure which is based on the size of the particles and may range from a gravel to a heavy clay.

Water content greatly influences plant life, and the powers of retention of water by the soil are related to its physical composition.

Humus content is both a physical and chemical characteristic and is bound up with water content and soil temperature. Types of humus, e.g. acid or basic, undecayed, partially or wholly decayed, are important.

The "lime" content of the soil is an important character, the presence or absence of calcium carbonate being estimated in the laboratory. Exchangeable calcium may be an important consideration in some problems. Degree of acidity or alkalinity may be expressed by a determination of hydrogen-ion concentration (P_H value).

Biotic Factors. The influence of animals and of man upon vegetation is the main theme of this work. The biotic factor is not entirely mechanical, but may be indirectly climatic, edaphic or physiographic according to whether animal and human activities produce "local climate," affect the chemical and physical composition of the soil, or produce changes of contour.

Physiographic Factors. These factors are inter-related with climatic and edaphic factors, and are concerned with the contour of the area and its geodynamics.

Estimation of Habitat Factors.

Climatic Data. There is usually a source of data in any neighbourhood from meteorological stations maintained under various organisations.

For determination of light intensity when comparing lighted or shaded habitats the only instrument yet utilised is the ordinary photographic actinometer. There are several drawbacks to this instrument. Light intensity is not constant throughout the day or the year due to obvious reasons, but taking all these facts into account useful comparisons may be made, though it is not known that the rays most effective in darkening the paper are not necessarily those most effective on plants.

In taking readings care has to be taken in shaded habitats to neutralise "sun flecks" by moving the actinometer during exposure. The instrument must always be horizontal to the source of light.

The method employed in making comparisons is to compare the lengths of time taken to darken the paper to standard tint in one habitat with time taken in another, the average of several readings in each case being used. If the darkening of the paper in one habitat takes 5 seconds and in another 50 seconds, the strength of the light in the latter is said to be

$\frac{5}{50} = \frac{1}{10}$ that of the former.

Local humidity of the atmosphere may be estimated by wet and dry bulb thermometers or by the Livingstone atmometer cup.

Edaphic Data. The physical or mechanical analysis of the soil is sometimes necessary though generally in field work arbitrary comparisons will suffice. Laboratory methods have been unified by certain organisations into a universal system, the details of which need not be given here.

Estimation of the chemical components of the soil entails laboratory analysis, too lengthy to describe. A chemical analysis in itself is not always of much value, unless interpreted in the light of a full understanding of all other factors.

Soil acidity must be considered in connection with some problems, and data may be obtained by use of the "lime requirement" method, (a laboratory estimation) which attempts to estimate acidity on the basis of the amount of "lime," calcium hydroxide, $Ca(O.H)_2$, required to neutralise the acidity of a given quantity of soil. This method has several drawbacks in the case of certain types of acidity.

The intensity of acidity or alkalinity (hydrogen-ion concentration) may be estimated by colorimetric means, employing certain indicators. There is a laboratory method for work requiring estimation of close ranges of P_H values, and a field method employing "Universal Indicator" for less exact work.

Soil moisture may be determined in the field by the "Hardy's Graphite Pencil" method, comparisons being made between the increases in weight, due to absorption of water, in graphite pencils placed in the soil of the habitats, or parts of the habitat, for a given length of time. This method has many pitfalls, and is not adopted in this work.

*The most general method for the estimation of soil mositure is by air and oven drying. The estimation is made in two fractions. Ten grammes of fresh soil (collected in sealed tins) are weighed out and air dried until of constant weight. They are then dried to constant weight in an oven at 100°F and the further loss recorded. Both air dry and oven dry weights are expressed as a percentage of the original weight.

Organic matter content may be estimated by burning oven dry soil. The loss in weight representing organic matter or humus is recorded.

Biotic Data. No orthodox laboratory methods are existent for the determination of biotic influences. Instruments and methods must be devised to meet the occasion.

Physiographic Data. Ordinary survey methods and existing geological maps suffice to obtain any information required.

*

The "chresard" (Clements) or "growth water" (Fuller) determination, i.e. Total water content — wilting coefficient, is said to be the only one of true ecological significance. For the purposes of this work, however, "total moisture" estimation will serve to substantiate the cases in point.

Terminology and Technique Adopted in Present Work.

The Nature of the Investigation.

The object of this work is to present an account of the floristic composition and phenomena displayed by common types of semi-natural vegetation. These communities are in existence all over Great Britain and are of remarkable similarity in spite of the varying conditions of soil and climate. A few specific differences occur, but in some types of communities the species are constant for all parts of the British Isles, and the habitat factors appear to function in a similar way.

The phenomena resulting from the influences of the biotic factor, such as the production of similar life forms or habitat forms are, judging by reports, of the same nature in all parts of the world, with an inevitable difference in the species.

The survey of these types of vegetation, consists in bringing to notice conditions which may be observed in the most accessible places, and to confirm and substantiate any part of the description requires only the most cursory observation. The general survey is not therefore a matter presenting much difficulty.

The problems arising from the surveys must be investigated by intensive methods, and are necessarily confined to a small area of the country, i.e. the area in which the investigator is located. The communities upon which the intensive work is carried out must be compared with similar communities in other parts of the country, from time to time, to be certain that any condition which comes to light is not a purely localised one.

Procedure.

The procedure in the following work is to give a general description of these communities as they exist in Great Britain. This is followed by a detailed technical description of each type of community, based on intensive surveys of a number of typical examples.

The phenomena and problems displayed are investigated by an examination of all the factors concerned, and by a process of elimination definite conclusions are drawn. Findings are, where necessary, subjected to experiment or laboratory tests. This latter procedure is, however, not always possible as the complexity of conditions influencing a community produces a balance which may be upset if the community, or any part of it, is removed from its site.

Terminology.

With regard to nomenclature, the terms used to define communities and their arrangement are those described in this work as being approved by the British Empire Vegetation Committee and generally in use by ecological workers.

Raunkiaer's system of life forms is adopted and also the broad outlines of Warming's system of habitat forms.

Quantitative Investigation.

The floristic composition of the communities is evaluated by assessing the relative abundance, frequency and dominance of the species. In each case the findings are based on definite counts, by quadrat or other suitable method. Relative abundance of a species is expressed as a percentage of the total of the numbers of all the individuals of each species present, assessed as individual shoots or tillers. Frequency is expressed by the percentage of the total number of counts taken, in which the species occurs. Dominance is expressed by the approximate fraction of the area of the community occupied by the species, assessed on a broad and arbitrary scale, or by the method of a real percentage occupied by the species.

Qualitative Investigation.

Qualitative terms constancy, exclusiveness, sociability, vitality, periodicity and stratification are assessed by the methods already described.

Periodicity of a species has been taken as the periods of the year during which the shoots are sufficiently conspicuous to contribute to the configuration of the habitat and are not actually dead, or in a dormant condition.

Maps and Illustrations.

To illustrate phenomena as much use as possible is made of photography, but where this does not give sufficiently clear illustration, mapping or charting is resorted to. In all cases where a chart of the community is made, the units or the individual plants which are illustrated are the dominant or sub-dominant species only.

Zonation is illustrated by charts which are types of line transects. Stratification of shoot system does not enter into this work, but the bisect is employed in the case of root systems.

Methods Employed in Assessing Habitat Factors.

Climatic Factors.

With regard to climatic factors the only information necessary is with regard to light intensity and here all that is required is an expression of the difference between a lighted or a shaded habitat. The Watkins Bee Meter is the type of actinometer used.

Edaphic Factors.

As regards mechanical analysis, only broad distinctions are required and these are purely arbitrary.

Where chemical analysis was required this has been done in the laboratory by the kind assistance of the Advisory Agricultural Chemist, at The School of Agriculture, Cambridge.

Where soil acidity is estimated in the field, again only broad distinctions are required, and "Universal Indicator" is used.

Soil moisture is estimated by the air and oven drying method. As the moisture estimations are compared only with those on a similar soil type no mechanical analysis accompanies the determination.

SECTION

2

GENERAL SURVEY AND DESCRIPTION

GENERAL SURVEY AND DESCRIPTION

GENERAL SURVEYS AND DESCRIPTION

The situations whose vegetation is defined as semi-natural are footpaths, sidewalks, cart tracks, gateways, waysides, hedgerows, certain types of grassland, waste land, and the sites of building and engineering activities. Semi-natural areas lie midway between the natural and the artificial and in some cases no sharp distinction can be drawn, this applies particularly with grassland.

The types studied are spread over the face of the country. This fact bestows a great advantage on these investigations, in that one is surrounded by one's material, and further that a great deal of exposition becomes unnecessary. None the less it is an extraordinary fact that these areas have received no scientific attention worth mentioning, and the mass of interesting phenomena would appear almost to have escaped notice.

Darwin refers to some of the phenomena by a passing referdnce in certain works. The change in the vegetation on the cart tracks, where wagons have traversed virgin country, is mentioned in "The Voyage of the Beagle" (1). The contrast between the vegetation of footpaths and the surrounding ground receives a passing speculation in "Vegetable Mould and Earthworms" (2) which is referred to later in this work.

Clements (3) describes the vigorous growth of

Agropyrum glaucum as an indicator of disturbance on the roads through the sage brush on the Red Desert of Wyoming. He refers again (4) under the heading of "Construction Indicators" to the fact that disturbance will alter the vegetation of a locality and also in another work (5) to the "peculiar zonation" of vegetation at roadsides on the Great Plains.

Taking a certain type of site, such as a footpath or hedgerow, in any part of the country, the constancy of the dominant species and of their arrangement is remarkable. In view of the fact that edaphic, climatic and physiographic factors are not the same, one can only assume that the one constant factor, i.e. the biotic factor is the influence responsible for this similarity in the vegetation. It is one aspect of this factor, the mechanical aspect which, in its diverse actions, demands the greatest attention.

The following observations on semi-natural communities were made in parts of the British Isles since the year 1918. The localities visited varied as widely as possible as regards climate, soil and physiography. The localities referred to are Aberdeenshire, Perthshire and the Lothians in Scotland, the Lake District, Derbyshire, Nottinghamshire, Norfolk, Isle of Ely and Shropshire; North and mid-Wales.

Observations were also made in the Irish Free State in Co Dublin and Co Cork in the year 1918. These places include such diverse soils as those of mountain and fen, acid and calcareous soils, and climatic conditions differing as widely as the limits of the country allow.

Footpaths

The footpath is taken as one traversing grassland, though many exist which intersect bare ground or arable fields. The width of the path may vary from several yards, as is the case with paths on much frequented common land, to less than a foot on a mountainside.

The vegetation is usually shorter on the path than on the surrounding areas, though this varies with intensity of grazing. The most outstanding phenomenon is the dark green colour of the path in comparison with the other herbage. This deep colour is maintained throughout the year and is most conspicuous in winter when the path stands out in vivid contrast to the dead remains of plant life.

With the exception of paths on very dry sandy soil, the dominant species are Smooth-Stalked-Meadow Grass (Poa pratensis) Perennial Rye Grass (Lolium perenne) Wild White Clover (Trifolium repens).

Poa pratensis is constant for all examples and Lolium perenne for the majority. Trifolium repens is extremely scarce in shaded positions, but is constant for all paths exposed to sunlight. Crested Dogstail (Cynosurus cristatus) Cocksfoot (Dactylis glomerata) and Plantains (Plantago spp) are fairly constant.

A distinct and constant zonation is found. In the centre of the path, if much used, there is an area of bare earth. This is adjoined on either side by a zone of Poa pratensis followed by zones of Lolium perenne and Trifolium repens. An example of this is shown in Fig.2.Sec.3, this being a narrow path on a Lake-land fell (Tarn Howes.N.Lancs)

The surrounding vegetation is an Agrostis-festuca association with Briza, Vaccinium, Molinium and Nardus as sub-dominants, Fig.1.Sec.3, shows a small area of this and is a typical example of the contrast which occurs.

On dry sandy heaths in districts of low rainfall the dominant species are usually Festuca ovina, Agrostis stolonifera, Galium spp, Plantago spp and Hieraceum spp.

On heavier soils and in moister situations, where puddling of the surface occurs in winter, it is notable that the areas dominated by Poa pratensis and Lolium perenne are those where this surface puddling occurs. The sward is not broken, but the mud oozes through and almost covers the surface.

Sidewalks

Paved sidewalks are usually possessed of some vegetation except where they exist in the heart of a city or in the neighbourhood of chemical works or other places emitting fumes. Even city streets become greened over in the interstices between the stones or wherever bare soil exists, if the street is closed for any reason.

Different types of sidewalks are in use. Those which are asphalted will only possess vegetation at the kerb, or in any interstices on the other side. Flagged sidewalks in common with flagged garden paths usually shelter plant life between the flags, the interstices being filled with soil.

The remarkable feature of these sidewalks is the dominance and constancy of Poa pratensis. Where a flagged path adjoins a bank there may be many species on the bank but Poa pratensis is the only one which invades the interstices and withstands the treading with any degree of constance. Figs.24 & 25 Sec.3. shew a typical example.

Poa annua is occasionally found, but is more a transient species, springing into existence for a short time while the influence of treading is in abeyance. Agrostis spp. Sagina procumbens and Galium spp often occur as local dominants, but taking a number of examples other species are rare.

The dominance of Poa pratensis is in evidence in the most diverse localities. It has been observed as the dominant of the flags and kerbstones for miles along a road crossing Derbyshire moors, on the promenades of seaside resorts, in suburbs and in cities in all parts of the country.

In cases where flags exist and are not trodden, other species take the place of Poa pratensis. Fig.26, Sec.3, shews an example of this. The flags in this case lie level with the surface of a field on one side and a bank on the other. It will be seen that the dominant here is Trifolium repens.

Poa pratensis usually exists on sidewalks and flagged paths as a pure dominant stand. As the laying of the flags or stones is preceded by the removal of the previous community, this stand must be defined as a consocies.

Cart Tracks

Cart tracks, frequently used lanes and fen droves are all similar habitats as regards the mechanical aspect of the biotic factor. These places are in a constant state of disturbance during winter or wet weather. In summer the surface becomes hard and more stable.

Fen droves provide excellent examples of this type of habitat. Figs. 27, 28, 29, Sec.4, shew winter, vernal, aestival and autumnal periodicity of a fen drove. (Hilgay Fen Norfolk)

It will be realized that the disturbance due to the churning action of the cart wheels and horse's feet is not evenly distributed over the whole area, but certain regions will be comparatively undisturbed, e.g. the region between the horse's feet and the inside of the cart wheel, where the horse always pursues a uniform course (fig.34.Sec.4). These areas usually run in belts of uniform width or are elliptical in shape. In the case of a fen drove the whole surface may be disturbed in time, but often undisturbed areas exist.

The characteristic species of these areas are, Knotgrass (Polygonum aviculare) Swinescress (Senebiera Coronopus) Silverweed (Potentilla anserina) Greater Plantain (Plantago major) Rayless Chamomile (Matricaria suaveolens). The gramineous species are usually Poa annua, Poa pratensis, Lolium perenne, and associated with these Trifolium repens may be found.

Distinct zonation exists on these areas, and upon examination it is found that the most disturbed regions are dominated by the annuals while perennials dominate the more stable regions. The most severely trodden and compressed portions of the stable surface do not, as a rule, support gramineous species, but the least trodden and compressed part of the stable surface and the margins of the habitat may be dominated by the gramineous perennials and by Trifolium repens.

This community may usually be defined as an associes. The magnitude of the area and its separation by ditches or hedges from the surrounding communities should entitle it to this rank. It contains consocies, socies and colonies. It is obviously in an unstable state.

Gateways

The region in and around a gateway exhibits similar flora to that of any of the regions in the preceding section, the constancy of these species also is the same throughout the country. The obvious reason is that the mechanical factor is again the most potent.

Gateways, especially where entering on to grass land, exhibit a zonation which gives an excellent example of specific changes in response to varying intensity of compression.

In the actual gateway mid-way between the posts is an area of bare ground where disturbance and treading are so severe that no species can exist, except during the cessation of this factor. Following upon this is a zone in which Polygonum aviculare and Matricaria suaveolens are dominants. Intermixed with the latter species, but extending further out, Plantago major is found and is a constant.

Transient individuals of Poa annua may occur over any part of the area at certain seasons, most commonly in winter and vernal periods. In the gateway of a pasture gramineous species exhibit a zonation consisting of the same species, and in the same zonal arrangement together with Trifolium repens, as on a footpath. The gramineous zones are furthest from the gateway and merge into the pasture.

Gateway communities may be described as associes, being subordinate communities in cultivated or semi-cultivated communities.

Waysides

The term wayside is intended to describe the area which exists between the metalled road and the hedgerow, wall or ditch, or where the road traverses "open" land such as a heath where no artificial boundary is present. The region may be defined as that consisting of a community differing specifically and in arrangement from that of the surrounding communities, and adjoining the roadway. It is commonly spoken of as the "grass verge".

At the present day and far back into history roadways have penetrated every type of country, from the plai to the mountain tops, from the forest to the edge of the sea coast. A complete list of the species of the wayside would embrace almost all the British Flora.

Gramineous species are the most abundant and frequent and are constant for all wayside associes. From data obtained in various parts of the country the most frequent grasses are Poa pratensis, Lolium perenne, Dactylis glomerata, Holcus spp, Arrhenatherum avenaceum, Bromus spp.

Of the non-gramineus species, the following are most frequent. Trifolium repens, Rumex Acetosella, Nepeta Glechoma, Bellis perennis, Anthriscus sylvestris, Aethusa Cynapium, Daucus carota, Polygonum aviculare, Urtica dioica, Cirsium arvense, Taraxacum officinale, Potentilla anserina Plantago spp, Senebiera Coronopus, Lamium album, Centaurea nigra, Achillea Millefolium, Ranunculus spp, Cerastium spp, Leontodon autumnalis.

There is no community of those studied which is more subjected to disturbances of every type, both intentional and accidental, than that of the wayside. While providing a field for the study of these influences, there is an attendant drawback in that these operations continue throughout the year. They are often not anticipated and owing to these facts successive studies are usually upset.

Despite the varying and numerous influences at work, regular zonation is observed with great frequency. In the absence of interference such as trenches or gravel heaps, the species dominating the zones and their arrangement are fairly constant.

When interference does occur it produces changes in the form of consocies, associes and colonies. Some waysides are in a constant state of disturbance while others- usually minor roads are often left in a comparatively stable condition.

In typical cases, the zonation at the edge of the wayside adjoining the road is similar to that of the footpath, commencing with a zone of Poa pratensis and followed by one of Lolium perenne with Trifolium repens.

In some cases the Poa pratensis zone is succeeded or intermingled with one of Plantago major, Matricaria suaveolens, and Senebiera Coronopus.

Where the margin of the wayside is not trodden, e.g. where there is a raised margin sharply defined, the species present is usually Festuca ovina.

The middle region of the wayside where undisturbed is generally dominated by Dactylis glomerata or Holcus spp. The former of these species is usually in scattered colonies, the latter in consocies.

The inner region of the wayside assumes in vegetation many of the characteristics of the hedgerow and the dividing line is arbitrary. The dominants of this area are Urtica dioica and Arrhenatherum avenaceum.

Disturbance of the wayside in the form of excavations or the deposition of material on the surface produces socies or colonies of annuals and of certain types of perennials. These may persist for some time after the disturbing factor has been removed or disappeared. Common examples are the colonies of Cirsium arvense appearing on gravel heaps.

For the purpose of this work the wayside is defined as an associes, though this is an arbitrary point.

Hedgerows

The dominant species of the hedgerows is the shrub or tree which composes the hedge. The Hawthorn (Crataegus Oxyacantha) is by far the most frequent component species, this is owing to its superiority over other species for the purpose. It is a quick growing and effective barrier and extremely pliable in the hands of the skilled hedger.

The other species utilised are the Blackthorn (Prunus spinosa) Elm (Ulmus campestris) Holly (Ilex Aquifolium) Maple (Acer campestre) Privet (Ligustrum vulgare) Beech (Fagus sylvatica) Hazel (Corylus Avellana) Ash (Fraxinus excelsior) Dogwood (Cornus sanguinea) Coniferous species are employed in certain parts of East Anglia.

It often happens that several species occur together to compose what is known as a "mixed hedge". This is generally due to neglect of the hawthorn hedge in the first place, but some of the species may be introduced by means of birds or vegetatively.

The shape and height of the hedge may vary at the desire of the hedger, and as will be seen later in this work the design of the hedge influences the species of the community Figs. 101-104, Section 5, illustrate some examples of shape.

The position of the hedge may vary, i.e. it may be situated upon a bank or on the level, at the foot of a bank or in a hollow. This again greatly influences the accompanying flora.

In the case of the hedgerow, as with the wayside, the influence of disturbance is great, but in the former instance there is the added effect of the hedger's operations, and of the "cleaning" of the hedgerow. This is usually an annual operation, but in highly cultivated districts may be carried out so intensely as to exterminate the whole of the flora excepting the actual hedge.

On stable and undisturbed hedge banks the most frequent gramineous species are, Festuca, spp, Agrostis stolonifera, Dactylis glomerata, Holcus spp and Arrhenatherum avenaceum. Grasses are in this case the dominants. Fig 81, 82, 84 Sect 5 are typical examples.

On disturbed hedge banks the flora appears to be directly correlated to the intensity of interference. Figs. 76 77, 78 Section 5, are illustrations of banks of this type. The most frequent gramineous species here are Agropyrum repens and Bromus spp.

Of non-gramineous species the most frequent are Urtica dioica, Lamium album, Cirsium arvense, Anthriscus sylvestris, Stellaria spp, Galium Aparine, Convolvulus sepium, Rubus fruticosus, Nepeta hederacea, Hedera Helix.

As in the case of the wayside, the complete flora is too comprehensive to include in this work, but it is more limited than that of the wayside in virtue of the fact that the habitat is more of a fixed type, being usually a bank dominated by shrubs.

The chief disturbance in the case of a hedge bank appears to be the deposition of earth in the form of mud and ditch or road cleanings. This is frequently pasted on almost vertical banks.

In some cases a neglected hedgerow, particularly where the hedge is of Ulmus campestris, will send out suckers which give rise to shoots dominating the bank. This may form a thicket, thus completely altering the community.

On a comparatively undisturbed bank (no bank is completely free from disturbance) the gramineous species exhibit a marked zonation. Festuca species occupy the lower region of the bank while Dactylis glomerata occurs in colonies about the middle region. Above the middle region and adjoining the hedge Arrhenatherum avenaceum is extremely frequent as a distinct zone. At the top of the bank in the actual hedgerow itself Holcus mollis, growing in the form of a climbing plant, may be present. Occasionally Agrostis stolonifera may exist in conjunction with Holcus mollis and exhibiting the same habit of growth.

On disturbed banks the zonation is often distinct though many species grow in consocies or colonies. Urtica dioica occupies the topmost region and extends outwards at points. Lamium album usually occurs in association with Urtica dioica, but the former generally occupies the lower and less shaded position. Colonies of Cirsium arvense exist at almost any point, except within a dense hedgerow. Bromus sterilis occurs in consocies and Hordeum murinum is found in colonies.

Climbing plants such as Galium Aparine and Convolvulus sepium may originate at any point, but the upper parts grow towards the hedgerow for support.

In the vernal period Anthriscus sylvestris is the most frequent dominant of the hedgebank, forming in many cases a zone occupying and obscuring the whole of the bank and hedgerow.

Other banks occur on busy roadways or in the suburbs where disturbance is almost continuous. Usually a hedge bank on a country road exhibits disturbed and undisturbed areas at different points of the bank.

The hedgerow and bank may be described as an associes. It is often difficult to draw a boundary between the hedge bank and the wayside, in fact the wayside may be absent and a bank fall straight to the road. The hedgerow associes is here regarded as a part of the wayside although hedgerows occur in fields and exhibit the same character as when adjoining the wayside.

Semi-natural Grassland

The definition of semi-natural grassland is somewhat artificial. Types such as moorland, mountain, salt marsh or heath are regarded as natural, having been in the main in an undisturbed state since times beyond record. Exceptions do occur where parts of these areas may have been cultivated in the past, but they have usually reached a climax in equilibrium with the rest of the area.

On the other hand there are artificial types of grassland known to agriculturists as "short term leys". In these cases a mixture of grass seeds or a single species has been sown, usually in conjunction with clovers. The resulting herbage is fairly well controlled as regards composition, and is eventually ploughed up and put under another crop.

Semi-natural grassland is for the purposes of this work regarded as that which has been sown for some time, and has taken in many of the characters and species of natural grassland. The term is also taken to describe grassland which was originally natural, but by utilisation has lost many of its natural characters, e.g. permanent pastures in contrast with heaths or mountain grazings.

Empirically semi-natural grassland may be classed under two main headings, "good" and "poor". The good grassland, which is usually classified as "milk producing" or "fatting", possesses a great similarity of character and flora in any part of the country. It will be found (with a few notable exceptions) that good grassland is characterisied by having as its most frequent species Lolium perenne, Poa pratensis, Poa trivialis, Dactylis glomerata, Cynosurus cristatus and Trifolium repens. This type of grassland is always found to be in good "physical" condition, the turf being described as "open", there being no matted mass of root material obscuring the soil. Earthworms (Lumbricidae spp) are always active, as evidenced by the abundance of worm casts. The arrangement of the species in these communities of "better class" pastures is comparatively homogeneous the species being well distributed.

In the case of poor grassland there are two main types. In one case the herbage may be of the thin degenerating type, where the covering is scanty. This type is somewhat unusual and is produced by some chemical or physical defect in the case of the edaphic factor, or by the climate or physiography, or by certain aspects of the biotic factor such as overgrazing.

The most frequent type of poor grassland is the "matted" type where for certain reasons partly edaphic, but mainly biotic such as uncontrolled grazing, a mass of root material occurs on the surface of the earth which is known as a "mat" or "skin." In this type of grassland the herbage consists of the species tending to occur in consocies or colonies.

In the case of all poor grassland the dominant and most frequent species are Agrostis spp Festuca spp and Holcus spp.

Lawns are studied as a type of semi-natural grassland. They appear to owe their characters mainly to the biotic factor, i.e. the close mowing as distinct from disturbance, deposition and compression.

The most frequent species in the case of lawns are Holcus spp, Agrostis spp, Festuca spp, Poa spp, Galium saxatile Cerastium spp, Bellis perennis, Plantago spp. These species tend to form consocies and colonies.

Waste Land etc.

Waste land and the site of engineering operations, in conjunction with railway embankments, possess so many diverse characters that they are not given a separate section, but railway embankments and slag heaps are briefly described here.

Ditches exhibit a type of semi-natural vegetation, but as they constitute a study of a specialised nature, and of great magnitude, they are not considered in this work.

Railway Embankments

These areas, like the wayside, possess a very wide variety of species according to the type of country through which the railway passes.

Frequently the vegetation is similar to that of a cli face. Where there is a covering of soil the gramineous species are present, the dominants being Festuca ovina, Agrostis sp Dactylis glomerata, Arrhenatherum avenaceum occurring in the above order with increasing depth of soil.

Where there is a loose subsoil or clay in the absence of hard rock and where topsoil is absent or scarce the dominant species are geophytes, e.g. Tussilago Farfara, Cirsium arvense, and Equisetum spp.

Where a cutting runs from East to West, the land with the southern aspect is usually more thickly covered with vegetation and composite species are more abundant.

For obvious reasons no counts could be taken, but observations were frequently taken by what is known in the U.S.A as "car window ecology."

Slag Heaps

These heaps occurring on the sites of collieries, iron works or chemical works are frequently devoid of vegetation. This may be owing to the chemical nature of the heap, to heat within the heap or to chemical fumes in the vicinity.

Where there is a thin covering of soil, Festuca ovina and Agrostis spp with an occasional colony of Holcus mollis may be found. The most frequent non-gramineous species are, however, Epilobium spp.

SECTION

3.

THE VEGETATION OF FOOTPATHS AND SIDEWALKS

THE VEGETATION OF FOOTPATHS & SIDEWALKS.

The Vegetation of Footpaths.

The footpath may be defined as that area of ground which comes under the influence of the treading action of individuals moving in either direction between two points. The plant community affected by this factor is in the case of the present work, that of grass land.

The footpath will be of variable length, according to circumstances, but the width is obviously limited, and ranges from several inches to a number of yards. On public grasslands the path is usually wide, while in meadows where a crop may be damaged, or on a mountainside where foothold is precarious, it is narrow.

Treading is found to be more concentrated on the centre of the path, and not evenly distributed. This is probably due to the habit or instinct of individuals, who tend to follow the footsteps of others or take the straightest line between two points. Paths usually pursue a straight line, but a winding course may be taken owing to obstructions or uneven contour of the ground. Frequently a footpath splits into several branches, each possessing the distinctive characters of the community, and converges again at a further point. This is also due to obstruction or uneven contour, past or present.

While the length is definite in each case, the limits of width are not sharply defined and merge gradually into the surrounding community. The boundary is usually found to occur where the Lolium perenne and

Trifolium repens zone reaches its outer limit. See fig. 2.

Floristic Composition.

The flora of the footpath and its arrangement into zones, which are more or less clearly defined, has already been described. The figures in the following tables, and the illustrations of the relative area occupied by the species by columns representing areal percentage, give concrete facts presented in statistical form.

Counts were taken to determine the relative frequency and area occupied by the species, but it was necessary to devise a means of distinguishing between the footpath socies proper and its surrounds. When the quadrat fell on the margin of the socies it was included in the counts, provided more than half of its area was adjudged to be within the community. If more than half was in the surrounds it was discounted. By this method a certain number of species were included which are not typical of the footpath proper, but a clear idea of the true state of affairs is presented by the photographs, Figs. 1 and 2.

Table. I. presents quantitative data regarding 8 examples chosen from different localities and different types of soil. Percentage frequency (dispersal of the species) and percentage area occupied (dominance) are given for each species of the footpath community, and this is compared in each example with similar data of the surrounds.

In the case of communities such as those under

Erica cinerea																											7	5			[illegible]	[illegible]
Galium saxatile							49	25																			50	12	24	4	8	6
Pteris aquilina																											6	6			38	20
Hieraceum spp																									33	8	16	2				
Rumex Acetosella																															6	12
Plantago major	41	8							22	7			27	6			27	7			71	8										
Plantago Coronopus																									43	4			78	7		
Plantago media																									21	4	7	2				
Plantago lanceolata	20	3																									12	2				
Urtica dioeca																							17	21								
Lamium album																							7	7								
Daucus Carota																							13	6								
Luzula spp																											18	5				
Mosses																															20	8
Miscellaneous			7	5			5	5			8	5			5	7			9	7							40	8			8	6
BARE GROUND	61	27			30	26			60	29			21	13			31	15			31	4			12	7			17	21		
Total	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100

TABLE I. EIGHT EXAMPLES

SPECIES	EX.I.				EX.II.				EX.III.				EX.IV.				EX.V.				EX.VI.				EX.VII.				EX.VIII			
	Silurian				Silurian				Coal Mures.				Boulder Clay				Silt				Alluvial				Chalk Soil				Greensand			
	Sheep Walk				Larch Wood				Mixed Wood				Paddock				Marsh pastre				River-side				Chalk Heath				Sandy Heath			
	Path		Srnds		Path		Srnds		Path		Srnds		Path		Srnds		Path		Srnds		Path		Srnds		Path		Srnds		Path		Srnds	
	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequence	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency	Areal % age	Frequency.	Areal % age	Frequency	Areal % age
Poa pratensis	72	41	-		100	74			83	40	10	7	79	44			39	17	47	8	84	27			92	30			3	2		
Lolium perenne	61	8							61	16			61	7			96	47	84	19	91	47			69	17			2	1		
Dactylis glomerata													10	6	25	15		7														
Cynosurus cristatus	36	6															13	3							63	7	29	8				
Trifolium repens	32	7							9	8			39	24			61	11	81	27	33	10			72	18			4	2		
Agrostis spp			73	30							92	48			86	45							57	26			75	17	88	44	8	8
Festuca ovina			90	18											67	15											82	30	61	17	42	10
Festuca elatior															13	5							10	7	17	5						
Holcus spp											41	30			61	13			24	14			37	18			20	5	3	2		
Poa trivialis																			21	18			13	7								
Aira caespitosa											10	10																				
Deschampsia flexuosa							100	70																								
Briza media			13	16																												
Erica cinerea																																

consideration, where dense tillering species like Festuca ovina are mixed with large single shoot plants like Pteris aquilina, any expression of relative abundance is misleading and useless, this is therefore omitted.

Table.II.gives a qualitative description of each of the species of the community. In this table the characters, constancy, exclusiveness, sociability, vitality and periodicity of the species of the footpath are expressed. In the case of constancy, sociability and periodicity, both the species of the footpath and the surrounds are represented and their behaviour in each locality compared. In the case of the characters exclusiveness and vitality no useful purpose would be served by comparing the species of the footpath and surrounds, and only the footpath is dealt with.

Table III is a diagrammatic illustration of percentage area occupied by the species of the footpath and of the surrounds as expressed in Table II.

Examples I, II, III & IV, Table.I, have been published in the year 1929 (6), but in the present instance they are presented in a more detailed form after a re-survey of the areas. The chief modifications being that the re-survey was carried out during summer months, (when Plantago spp were present), and bare ground was included in the survey.

Line or belt transects or maps of the surrounds would serve no purpose and in the case of the footpath itself the limited dimensions of the area make

	Constance		Exclusiveness	Sociability		Vitality	Periodicity	
Bellis perennis	25	87	Preferential.				-	do.
Pteris aquilina	0	9	-	2-3-4	2-3-4-5	-		
Hieraceum spp	12	6	Preferential	2-3	2-3-4	⊙	do.	do.
Rumex Acetosella	2	22	Accidental	-	2-3-4-5	⊖	do.	do.
Plantago major	89	12	Preferential.	1-2-3	1-2-3	●	do.	do.
Plantago Coronopus	12	5	Preferential	1-2-3	1-2	●	do.	do.
Plantago media	22	26	Indifferent	1-2-3	1-2	●	do.	do.
Plantago lanceolata	20	18	"	1-2-3	1-2	●	do.	do.
Urtica dioica	0	6	-	-	2-3-4-5	-	-	do.
Lamium album	0	6	-	-	2-3-4-5	-	-	do.
Daucus Carota	0	8	-	-	2-3-4-5	-	-	do.
Luzula spp	2	20	Indifferent	2	1-2-3-4-5	●	do.	do.
Mosses	4	21	Accidental	--	2-3-4-5	⊖	V.ae.au.W.	V.ae.au.W.

Constance: Number of cases in 100 examples in which species occurs.

Exclusiveness:
5.) Exclusive-almost confined to a given community.
3.) Preferential -preferring one community, though growing more or less abundantly in others.
2.) Indifferent-preferring neither one community nor the other.
1.) Accidental-accidental

Sociability:
1 - single shoots.
2 - shoots in small groups
3 - shoots in larger groups
4 - shoots in small colonies
5 - shoots in pure populations.

Vitality:
● = complete cycle regularly accomplished.
⊙ = Cycle usually incomplete. Vigourous vegetative developement.
⊖ = Cycle incomplete restricted vegetative developement.
O = Germinating accidentally not multiplying.

Periodicity:
V = Vernal = (Spring)
AE = Aestival = (Summer)
AU = Autumnal = (Autumn)
W = Winter = (Winter)

Table II

A v e r a g e of 100 E x a m p l e s

S P E C I E S	% Constancy		Exclusiveness	Sociability		Vitality	Periodicity	
	Path	Surrounds	Footpath	Path	Surrounds	Footpath	Path	Surrounds
Poa pratensis	100	68	Preferential	5	2-3-4-5	●	v.ae.aw.w.	v.ae.au.aw.
Lolium perenne	100	88	"	4-5	2-3-4-5	●	v.ae.aw.w.	v.ae.au.aw.
Dactylis glomerata	34	·86	Indifferent	2	2-3-4-5	Θ	v.ae.aw.-	v.ae.au -
Cynosurus cristatus	36	78	"	2	2-3-4-5	●	v.ae.aw.w.	v.ae.au. w.
Trifolium repens	80	96	Preferential	4-5	2-3-4-5	●	v.ae.au.-.	v.ae.aw. -.
Agrostis spp.	21	84	Indifferent	2-3-4-5	2-3-4-5	⊙	do.	do.
Festuca ovina	20	62	"	4-5	2-3-4-5	⊙	do.	do.
Festuca elatior spp	4	27	"	2	2-3-4	Θ	do.	do.
Holcus spp	18	69	"	2-3-4	2-3-4-5	Θ	do.	do.
Poa trivialis	0	35	Accidental	-	2-3-4-5	-	-	do.
Aira caespitosa	2	10	"	2	2-3-4	Θ	do.	do.
Deschampsia flexuosa	3	6	"	2-3	2-3-4-5	Θ	do.	do.
Briza media	0	4	"	2	2-3-4	-	-	do.
Molinia caerulea	0	4	"	2	2-3-4-5	-	-	do.
Nardus stricta	0	5	"	2-3	2-3-4-5	-	-	do.
Bellis perennis	25	87	Preferential	2-3-4	2-3-4-5	[illegible]	[illegible]	[illegible]

photography possible, and the phenomena may be readily examined in nature. The photographic illusrations Figs. 2 and 3, accompanied by a descriptive account of conditions (Section 2), give a more faithful representation of the arrangement of the footpath community, and the area occupied by individual species, than could be obtained by a line or belt transect.

It will therefore be seen that the methods of presenting the conditions of the community and the nature of the problem are broadly those described in Section I of this work, dealing with "Definitions and Technique", with the modifications necessary for the particular case in point.

An examination of these tables shows that with the exception of Example VIII the dominants of a footpath are Poa pratensis, Lolium perenne, Trifolium repens with Plantago spp. The latter are abundant in Example VIII.

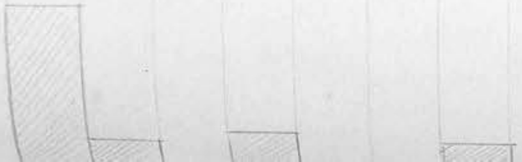
The inclusion of Example VIII in taking the average for the purpose of Table III greatly exaggerates the average dominance and frequence of Agrostis spp and Festuca ovina. This would appear to be a departure from the typical Poa pratensis, Lolium perenne and Trifolium repens community of the path, but paths of the type of Ex.VIII do not occur to the extent of 1 in 8. In a survey conducted in the Midlands in 1929 (7), out of 50 examples only two were found where the habitat was dry, and in these cases it was an artificially dry condition. In Example. I. Fig. 2, the path occurred on a steep hillside where the soil was thin and stony, but owing to the high rainfall of the district puddling occurred and consequently the typical

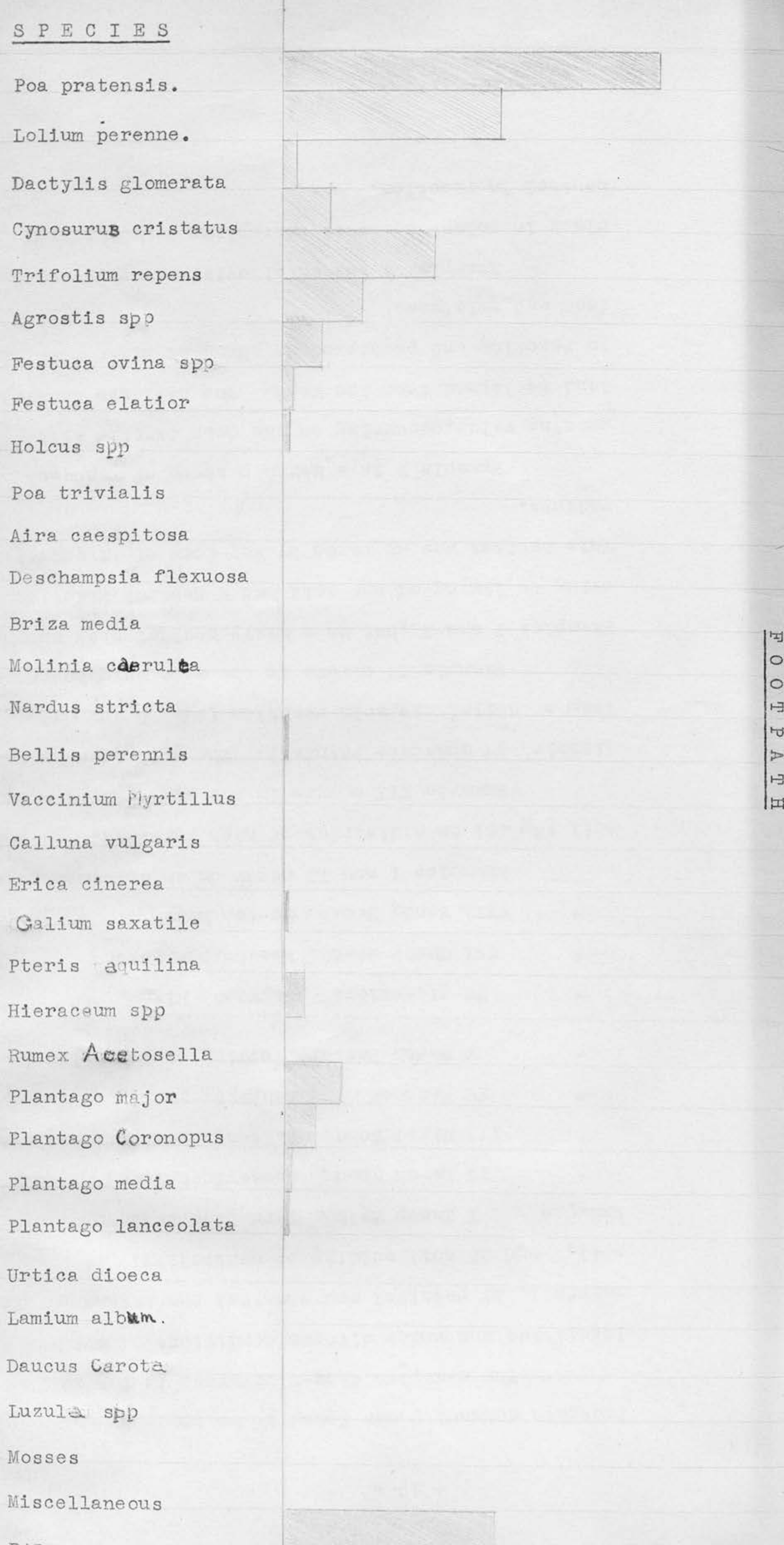
TABLE III

DIAGRAMMATIC REPRESENTATION OF AREA OCCUPIED BY SPECIES ON THE FOOTPATH AND SURROUNDS

(Average of 8 Examples of Table I)

SURROUNDS




SPECIES
Poa pratensis.
Lolium perenne.
Dactylis glomerata
Cynosurus cristatus
Trifolium repens
Agrostis spp
Festuca ovina spp
Festuca elatior
Holcus spp
Poa trivialis
Aira caespitosa
Deschampsia flexuosa
Briza media
Molinia caerulea
Nardus stricta
Bellis perennis
Vaccinium Myrtillus
Calluna vulgaris
Erica cinerea
Galium saxatile
Pteris aquilina
Hieraceum spp
Rumex Acetosella
Plantago major
Plantago Coronopus
Plantago media
Plantago lanceolata
Urtica dioeca
Lamium album.
Daucus Carota
Luzula spp
Mosses
Miscellaneous
FOOTPATH

footpath community was found to be present.

The examples chosen occurred in the following localities and under diverse conditions of climate and rainfall, of physical and chemical conditions of the soil, and of soil acidity or neutrality.

Example	I Sheep Walk.	Tarn Hows, Hawkshead, Lake Dist^t.
"	II Larch Wood.	Gooseyfoot Tarn, " " "
"	III Mixed Wood.	Walton, Chesterfield, Derbyshire
"	IV Paddock.	Ashgate, "
"	V Marsh Pasture.	Terrington Marsh, King's Lynn, Norfolk.
"	VI Riverside.	Gaywood River, " "
"	VII Chalk Heath.	Massingham Heath, " "
"	VIII Sandy Heath.	Wooton Heath, " "

Examples I and II occur on an acid mountain soil (P_H .4) in a district of high rainfall.

Example III occurs in the Midlands in a district of moderate rainfall. The soil is a medium loam of definitely acid reaction (P_H. 5 approx).

Example IV occurs in the same neighbourhood as Examples I and II, but on a heavy boulder clay which owing to liming of the soil had a neutral reaction. This habitat was ungrazed by any form of livestock or rodents.

Example V is a marsh pasture of renowned grazing value, occurring on the deep fertile silt land reclaimed from the Wash. The soil was neutral in reaction and possessed an abundant reserve of plant food and moisture.

Example VI was an alluvial riverside soil, black in colour somewhat resembling fen, and was neutral in reaction.

Example VII was that of a footpath traversing a heath overlying chalk, and adjoining a cart track along which chalk had been carted for many years. The habitat was comparatively a moist one and the soil neutral in reaction.

Example VIII was that of a path traversing a sandy heath overlying the Lower Greensand formation. The habitat was very dry and the soil acid in reaction (P_H. 5 approx).

Fig.1, shows the type of surrounding vegetation in Example I, and Fig. 2, shows the footpath flora in the same example. In the latter case the zonation of the species is clearly seen. This is a very typical example.

Fig. 3, shows an example of the sandy heath in Example 8, and Fig. 4, the characteristic flora of the footpath in this case.

Habitat Factors.

Edaphic Factors.

Physical Conditions: The soil of the footpath is in the first place similar to that of the surrounds, and would exhibit the same character upon mechanical analysis. Any differences in the physical condition of the soil of the two areas are the result of the treading upon the path.

It is obvious that the soil of the path possesses a greater density, due to the compression, than that of the surrounds. * Attempts to obtain definite measure of the respective densities were a failure and only approximations were possible. This was due to the difficulty in exact excavation, owing to plant roots and to stones. Several facts were, however, quite apparent from the investigation.

In the case of the surrounds the top five centimetres were of lower density than those below, owing to the lightening effect of plant roots, and also to the fact that there is no superimposed layer of soil, and that no treading occurs.

In the case of the footpath the surface soil is of greater or equal density to the lower soil. The lower soil was about the same density as that of the lower soil of the surrounds.

It would appear that in the case of the footpath, the denser or consolidated condition of the soil, due to treading, exists only in about the first 3 to 5 cms, and that below that level conditions are comparable with those at a similar depth in the remainder of the field.

* Data are given in Sec 10. as to the secondary influence of the compressed surface upon temperature and moisture conditions.

This surface consolidation or "crusted" condition of the surface does in itself exert an influence on the habit of growth of certain species existing upon it. This is fully discussed later. (See. Sec. 10.)

The exact arrangement or texture of the particles in the surface layer will differ according to whether the trodden soils contain a certain proportion of clay or not. Clay when trodden or "puddled" in the presence of moisture becomes altered physically, owing to deflocculation of the particles. The result of this action is the retention of moisture on the soil surface, and upon the soil drying by the evaporation of this moisture, a "baked" or "poached" condition arises. A crust of varying thickness and of a hard baked nature is produced.

*The proportion of clay in the soil of the footpath and the condition arising therefrom cannot be of any importance as a factor influencing the production of the footpath community, for the community is the same in its main features on other types of soil.

Experiments were carried out in the year 1929 on a heavy loam soil (Chesterfield, Derbyshire), and again in 1932 on light sandy loam (Nr. King's Lynn, Norfolk) in an attempt to determine whether consolidation in itself exerted direct influence or selective influence on the species.

A garden border was in each case divided into two, one half was consolidated and one left loose. The following species were sown in rows (duplicated

* Except in the extreme case of dry sandy heath.

and randomised) across both loose and solid areas. Lolium perenne, Poa pratensis, Holcus lanatus, Agrostis stolonifera, Festuca ovina, Trifolium repens and Plantago major

In the case of the 1929 experiment the soil was consolidated to a depth of about 30 cms. by packing the soil layer upon layer. *In this experiment it was found that all the species were reduced to about half the size and weight of those upon the loose soil. The root systems were also restricted by the solid soil. (8)

In the 1932 experiment, consolidation was carried out by surface pressure after the species were established, care being taken not to crush any of the leaves or stems of the plants. In this case the consolidation resembled the type effected on the foot-path, i.e. only the first few centimetres of soil being affected. In this experiment little result was noted, except in the case of Poa pratensis which was reduced in size in the consolidated portion. Holcus lanatus, Agrostis stolonifera and Festuca ovina appeared also to be slightly reduced in size. It appears significant that these species are comparatively shallow-rooted.

From the above results there appears no reason to suppose that consolidation in itself is responsible for the "footpath flora." Poa pratensis is the species most adversely affected and yet this is the constant and most abundant species upon the most consolidated part of a path.

* Gupta (40), growing plants in consolidated soil, noted root range restriction, but did not obtain such marked decreases in total weight. It is possible that in the writer's experiment, the close packing of the soil in a moist condition, as contrasted with packing in a dry state, was responsible for the differences.

Soil Moisture.

* On the whole the footpath is a moister habitat than the surrounds. † The pressure of the soil particles into closer association increases surface tension and consequently increases the power of a soil to retain moisture. The footpath surface is compressed to a lower level than the surrounds and gravitation will increase water supply in virture of this fact.

It frequently happens that the vegetation of the surrounds is matted and this surface covering of root material, as shown later, retains water at the surface and renders the soil dry. On the footpath "mat" is eliminated by treading and a more free access of water is possible.

On the other hand a clay soil may, in the puddled state of the footpath, prohibit the access of moisture, and may bake very hard in dry weather. Moisture conditions will be worse, in such cases, on the path than on the surrounds, yet the footpath still possesses its distinctive vegetation.

The species of the footpath socies are not, as a whole, characteristic of a wet or dry habitat. Lolium perenne thrives under good moisture conditions, but is deep rooted and fairly drought resistant. Poa pratensis is shallow rooted, but possesses underground runners and is drought resistant. This latter grass is recognised by agricultural botanists as one which tolerates dry situations. Trifolium repens is, in virture of its deep root system, very drought resistant, and it is often to be observed that when pastures are burnt dry, this species is still present

* For data see section 10.

† In some recently published work it has been shown that consolidation does not greatly affect water holding capacity. (40)

in a green state. In fact a dry season favours the development of Trifolium repens.

In view of the above considerations it does not appear that moisture in itself can be regarded as a factor which is directly responsible for the existence of a distinct footpath socies. It is asserted by some that the deep green colour of the footpath in winter is due to moisture, but this may be explained by the fact that the species of the footpath are all evergreen or "winter green."

It is a striking fact that the footpaths existing on dry sandy soils in districts of low rainfall do not possess the characteristic flora of paths in other situations. Figs. 3 and 4. Small colonies of Poa pratensis and Lolium perenne may be found in the damp hollows, but the dominant and subdominant species are Festuca ovina, Agrostis stolonifera, Galium spp. Plantago spp (excluding Plantago major) and Hieracium spp (e.g. Example VIII) The phenomena were also noted when paths traversed a cinder track and a slag heap. (7)

On all other types of soil in moister situations the characteristic footpath community exists on an area which coincides exactly with that which is puddled on the surface in winter. As already stated the sward is not broken, but mud oozes through and becomes mixed with the herbage.

The incidence of the typical footpath community of Poa pratensis, Lolium perenne, and Trifolium repens with the puddled areas is highly significant, and goes to show that a moist condition of the soil is an important, though certainly indirect factor. Example I Table I. occurred on a steep hillside with a thin stony open soil, but the rainfall was very high and consequently puddling took place, resulting in the characteristic community.

The presence of moisture and a suitable physical condition of the soil are essential to puddling. This action appears to have a direct bearing on the species Poa pratensis and Lolium perenne. It may therefore be considered that moisture is an essential though indirect factor influencing the footpath socies, in that moisture is essential to puddling and as will be seen later this section is essential to the production of a footpath socies.

Chemical Composition. There is no reason why the chemical composition of the soil of the footpath should vary from that of the surrounds. There is a possibility, in some cases, of a greater accumulation of organic matter from decayed vegetation on the surrounds than on the footpath, but this is not always the case.

Grazing animals prefer the footpath, and in consequence it may receive more droppings and urine than the surrounds. It is to be noted however that in the case of some paths, livestock and even rabbits are excluded, e.g. Example IV Table I.

As regards soil acidity a number of investigations failed to reveal any significant difference in the P_H value of the soil of the surrounds and the path, except where much "mat" was present on the surrounds, and here a difference was recorded, the earth below the "mat" being more acid than that of the path..

Light and Aspect.

When a footpath traverses grass land there is greater illumination on the path than on the surrounds, owing to the fact that the herbage is suppressed by treading, and its shading effect thereby removed.

In any cases where a path runs E to W the north margin of the path (which faces south) will be illuminated by the direct rays of the sun at its maximum intensity. The opposite side, especially where overshadowed by tall grass or raised ground, will be shaded.

The difference in illumination determined by actinometer was for the shaded portion $\frac{1}{9}$ that of the lighted northern side, in a typical example.

Light intensity exerts a marked influence upon Trifolium repens. In a shaded habitat, such as a wood or where other bodies exclude sunlight, Trifolium repens is absent or very scanty (e.g. Example II Table I)

Even aspect affects this species, and it will be found that where the southern side of a path is shaded from direct sunlight by tall grass or rising ground there is a considerably lower scale of abundance, frequency and dominance, than on the opposite side.

The following is a typical example of this phenomenon (Characters, column 3, expressed as 100%)

TABLE IV

Average of 10 Footpaths (Near King's Lynn).

Direction E - W.

(Ground rising slightly on southern side).

1 Species	2 Characters	3 Southern Aspect	4 Northern Aspect.
Trifolium repens.	Frequency.	100.0%	56.3%
" "	Abundance	100.0%	13.4%
" "	Area covered	100.0%	24.8%

When Trifolium repens is in flower, the relative abundance of white flower heads on the side of a path with a southern aspect to that with a shaded northern aspect is very conspicuous.

Light intensity does not appear to exert any marked influence in respect of the other species of the footpath, they may all be found in shaded situations.

The Influence of the Biotic Factor.

Grazing. It is notable that livestock prefer to graze the footpaths rather than the surrounds. This applies mostly to sheep and horses as these animals bite closely. It must be obvious upon consideration that grazing is a secondary influence. The species of the footpath are the best pasture plants in an agricultural sense and owing to the shortness of the plants offer a succulent herbage.

The droppings and urine from the animals is sometimes held responsible for the green colour of the path, as is the case with water supply.

In some cases footpaths occur where grazing animals, including rabbits, are excluded (e.g. Example lV Table 1). No difference is noted as a result of this.

Treading

The effect of treading upon the flora of a community is threefold, and is both direct and indirect. The indirect action has already been studied, i.e. the consolidation of the soil, and its influence upon the species. It has been shown that this is not responsible for the existence of a footpath socies.

The direct influences are those of puddling and treading upon the plant itself, and the mechanical effect or injury caused thereby. It is very obvious that many species are damaged and are often completely destroyed by the action of treading, while on the other hand the species of the footpath socies are comparatively immune to harm of this kind.

The reason for this immunity or resistance must obviously be due to some peculiarity of structure which the species possess in common, and which is not possessed by the species susceptible to injury.

An examination of the habit of growth of the dominant gramineous species, Poa pratensis, and Lolium perenne, shows a very striking and significant character possessed by these species and not by the species of the surrounds, i.e. the conduplicate stem and folded leaf section as compared with the rolled arrangement of the leaf in other gramineae *(excepting Poa spp, Dactylis glomerata and Cynosurus cristatus). An examination of this structure of leaf and stem shows it to be an excellent adaptation to resist injury, for the leaf and stem offer a flat surface to the crushing action of the foot. The conduplicate arrangement of the stem is of a similar mechanical structure to the leaf springs of a carriage.

†The life form of the gramineous species of the footpath is also distinct from that of the most frequent species of the surrounds. The gramineous species of the path constitute a synusia of cryptophytes, the buds being buried just below the level of the soil. The gramineae of the surrounds are mainly hemicryptophytes the buds being at ground level and two of the species, i.e. Agrostis spp and Holcus mollis may be chamaephytes, being possessed of aerial shoots.

Figs. 5 and 6A.B. illustrate the positions of the buds, in relation to soil level, of the species Dactylis glomerata, Poa pratensis, and Lolium perenne as compared with Festuca elatior, Agrostis stolonifera and Agropyrum repens (Fig. 7 A.B.C.)

The former group represents the cryptophytes of the path and the latter three species the chamaephytes and hemicryptophytes respectively of the surrounds. In the case of

* Dactylis glomerata and Cynosurus cristatus are quite frequent upon foothaths.

† The arrangement of the gramineous species into life-forms is a somewhat fine point. It might be argued that certain species described in this work as cryptophhytes or chamaephhytes respectively might all be grouped as hemicryptophhytes, but adhering rigidly to the position of their perennating organs as the criterion, there is no doubt as to which species tend to the crytophhytic habit and which to the chamaephhytic.

Agrostis the aerial buds are clearly visible, but Fig.83 Sec.4 gives a more definite example of this in a specimen of Holcus mollis from a hedgerow.

*It appears obvious that the double adaptation, i.e. the folded leaf and conduplicate stem with the crytophytic life form enables the plant to withstand injury. The leaf and stem is resistant to injury while the growing point is protected below the surface of the earth.

It has been noted that Poa pratensis occupies the zone of the most intense treading and is followed on the less trodden area by a zone of Lolium perenne. A comparison of the two species shows Poa pratensis to be better adapted than Lolium perenne to resist injury. In the former case the growing point is buried deeper in the soil and the plant propagates by underground stolons as well as by seed. The leaves of Poa pratensis are short, tough and concave in longitudinal and cross section. The leaves of Lolium perenne are longer and more flaccid.

It is notable that Poa trivialis though possessing much the same foliage characters as Poa pratensis is very rare as an occupant of footpaths. Poa trivialis demands a moist habitat, it is also surface rooting with buds above soil level.

Poa annua is a therophyte in life form while the above species are perennial. It is also injured by treading as the leaves, though folded, are of a fragile nature and the growing points are at ground level. Poa annua may occupy interstices where it is protected from treading, and it may

* See large photograph, attached to outer cover, at the end of this section.

also have a transient existence during periods when treading is for some reason suspended (9).

Of the non gramineous species Plantago major is well adapted to withstand treading. The leaves are broad and tough and occur in rosette form, the upper ones protecting the lower. On the footpath the plant is an ecad occurring here as a cryptophyte whereas on untrodden areas it is a hemicrytophyte with semi erect leaves. Fig.8, shews an example of this adaptation to treading, (a) is an average sized example of the hemicryptophyte form on untrodden soil, while (b) & (c) are typical examples of the cryptophyte form upon heavily trodden soil. It will be noted that in (b) & (c) the flowering stem is protected in its lower parts by leaves. The average size of the plant is much smaller upon the footpath than upon the surrounds. Similar phenomena to the above are noted in the case of both Plantago media, P.lanceolata and P.Coronopus.

Trifolium repens is least adapted of any of the footpath species, and it is a significant fact that it occupies the outer zone and invades the footpath from the surrounds. Light appears to be the greatest attraction to Trifolium repens and to account for its presence on the footpath.

The plant is a chamaephyte with surface runners, and does in virtue of the tough and prostrate nature of these runners exhibit a certain resistance to treading. The leaves are often injured by the process and are smaller in size upon trodden areas. Fig.15, shews the progressive decrease in size of leaf towards the area of most severe treading. This phenomena is fully dealt with later. (Section.8.)

Trifolium repens is not injured by even pressure (as contrasted with treading) to the same extent to which the gramineae are. This is discussed later with regard to an experiment with a steam roller, and is presumably due to the deep tap root as contrasted with fibrous roots of grasses.

Experiments upon the Influence of Treading

An experiment was carried out to test the theory of resistance to injury possessed by certain species and not by others (9). The following grasses were grown in separate and repeated strips:- Poa pratensis, Dactylis glomerata Lolium perenne, Anthoxanthum odoratum, Alopecurus pratensis and Agrostis vulgaris. The ground was then utilised as a garden path and trodden daily. Poa pratensis assumed a low dense habit, Dactylis glomerata and Lolium perenne were suppressed, but persisted. The three remaining species were exterminated by the treading. The experiment was carried out in 1929 on a heavy loam (Chesterfield, Derbyshire). Puddling took place during wet weather, though the work was carried out in summer.

A further experiment was carried out in 1931 on a light loam (Kings Lynn, Norfolk). The following species were sown in rows and the trial duplicated. Trifolium repens, Dactylis glomerata, Poa pratensis, Lolium perenne, Festuca elatior, Agrostis stolonifera, Agropyrum repens (the latter was planted in the form of runners). Figs.9 & 10, shew the plots prior to treading.

A pathway was trodden through the plots (Fig.11) and the species were subjected to a severe treading and puddling during a wet summer and autumn. Figs.12.13 & 14 shew the effect on the species and Figs.15-23 the appearance of each individual species. It should be noted that there was a resting period of three weeks before the taking of the final photographs (Sept.1st 1931) this allowed a chance of recovery. Trifolium repens was affected by the treading but not destroyed. The effect of treading in diminishing the leaf size is clearly seen, the leaves progressively diminishing in surface area towards the centre of most intense treading. (See fig 15.)

Dactylis glomerata, Poa pratensis and Lolium perenne were somewhat restricted in developement, but persisted and quickly recovered from the bruising action of treading by making fresh growth during the resting stage. Festuca elatior offered some resistance but eventually the buds in the centre of the plant, being above ground level, were destroyed. Agrostis stolonifera and Agropyrum repens were completely destroyed and in the latter case the runners appeared dead and shrunken.

It was noted that seedlings of Poa pratensis appeared all over the trodden areas, but were very dense in the region of the Poa pratensis strips. It is possible that some of the seedlings were those of Poa annua, but if this were the case they did not persist beyond the seedling stage, as no mature plants were identifiable.

The exact effect of treading was as follows:-
The original plants were broken down, and the leaves damaged in the case of all the species. In the case of Festuca elatior, Agrostis stolonifera and Agropyrum repens the buds at the base of the plants were trampled in the mud and damaged, but with Dactylis glomerata, Poa pratensis and Lolium perenne, these were protected beneath the surface of the soil. It appeared that the damage to the basal buds of Festuca elatior, Agrostis stolonifera

and Agropyrum repens only took place when the earth was wet and treading produced a pulpy condition.

Effect of Heavy Roller

An experiment was carried out on a large scale in Hardwick Park N.E.Derbyshire in 1929 (10) to test the effect of evenly distributed and heavy pressure as contrasted with treading and puddling of the soil by the foot. Half an acre of grassland was rolled with a ten ton steam roller for several hours. The gramineous species were killed or severely damaged, but Trifolium repens remained uninjured. In the former case the damage occurred mainly at the rootstock and to the fibrous roots, but the deep seated root system of Trifolium repens with its deep seated lateral roots escaped damage.

Special Influence of Puddling

Festuca ovina and Agrostis stolonifera appear capable of withstanding treading upon a dry footpath, but they do not tolerate puddling. The same applies with Galium spp. In each of these cases these plants are extremely stunted by the treading and the leaves are very fine. It is obvious that the stunted leaf of Agrostis and the setaceous leaf of Festuca ovina must be resistant to treading, and it is significant that these species are the dominants on dry footpaths. Many other xerophytic species occur on the surrounds but are not found on footpaths,and are all of a type which would be damaged by treading,being upright or fragile.

While Festuca ovina and Agrostis stolonifera are able to withstand the action of treading upon the leaf they are not able to withstand the slight surface disturbance caused by puddling, and the damage done by the bruising action of the foot or hoof when pressing into the surface soil.

These two species are chamaephytes and the growing points are on the surface of the earth, further than this they possess an extremely superficial root system forming a mat of root material at their base.

Large Scale Experiment on Influence of Puddling

The following account illustrates the effect of puddling upon an association of Festuca and Agrostis. An experiment was carried out in Hardwick Park, Derbyshire, on a large scale in the following manner (11). An operation aiming at the imitation of the action of the hoof in wet weather was carried out on about four acres of very matted grassland. The composition of this, assessed on the percentage area basis was:-

	Agrostis spp	35.4
	Cynosurus cristatus	24.6
	Festuca ovina	23.1
	Luzula	9.2
Miscellaneus	Lolium perenne) Trifolium repens) Ranunculus spp) Moss) Holcus lanatus)	7.7
		100.0

This sward was cut frequently in two directions by a disc-harrow, drawn by a tractor while the ground was very wet and rain was falling. The turf was worked into a morass of mud and presented a puddled appearance. It was then heavily rolled.

The operation was carried out in March 1929 and in the following summer a complete change in the flora was noted. The analysis of the treated portion was as follows:-

	Poa pratensis	50.9
	Cynosurus cristatus	21.7
	Agrostis spp	9.1
	Trifolium repens	12.0
	Lolium perenne	1.0
Miscellaneus	Holcus lanatus) Festuca ovina) Ranunculus spp)	5.3

This sequence of events is illustrated in Figs. 142- 146, Section. 11

The above analyses were carried out independently by Mr.A.Roebuck (Advisory Biologist)of the Midland Agricultural and Dairy College

The influence of this puddling action,carried out by implements on a large scale,shows a result of such striking similarity to that observed on the footpath, as to need no elaboration. Festuca and Agrostis are almost destroyed.

It would appear probable that the evergreen or "winter green" condition of the species Poa pratensis and Lolium perenne may be a factor in their favour in that they are in a growing state during the puddling process. This may exert some influence, but in the above experiment the time of the operation (i.e.March in a moist warm spring) allowed a good chance for Festuca ovina and Agrostis stolonifera to recuperate.

Selective Influences of Treading and of Puddling.

From a consideration of the above dissertation, it would appear that the species which are found on footpaths in wet or dry situations are enabled to persist by virtue of their leaf structure. When , however, puddling becomes a factor, Festuca ovina and Agrostis stolonifera are obliterated, but all species possessing the cryptophytic life form are able to persist.

The effect of deeper puddling and disturbance than that which occurs on a grassland footpath is discussed later in this work. (Section 4.)

+The influence of treading and puddling upon a gramineous community may be readily demonstrated by rubbing a given area with a rubber squeegee during wet weather or when the ground is in a wet condition.

An experiment was carried out on Massingham Heath, Norfolk (Aug. 1932)

Three quadrats were chosen each 1 sq. metre in area and possessing a botanical composition of the species Agrostis stolonifera, Festuca ovina, and Holcus lanatus, as co-dominants, and scattered individuals of Lolium perenne Trifolium repens and Plantago spp.

The areas were rubbed with a squeegee and with the foot until the vegetation was bruised and the surface pasted with mud.

Several days later it was noted that the quadrats presented, as a whole, a dead appearance. It was noted, however, that while Agrostis stolonifera, Festuca ovina, and Holcus lanatus were apparently dead, the "stumps"

+ Figs: 23 A&B, show the same treatment carried out with a rubber implement (described in Sec: 11) on a large scale, during wet conditions.

of Lolium perenne and Plantago spp stood out of the ground in a striking manner and were still green. The runners of Trifolium repens were also still green.

A fortnight later it was noted that some of the Agrostis stolonifera shewed signs of recovery, a few fresh green shoots having arisen, but Festuca ovina had not recovered and Holcus lanatus was obliterated beyond recognition. (It is well known to horticulturists that to roll a fescue sward in wet condition is fatal to the species).

Lolium perenne had made a good recovery having grown leaves up to 10 cms long. Trifolium repens was developing leaves and this was also the case with Plantago spp.

The Formation of the Footpath Socies

In the years 1929-30, in a grass paddock (Hawkshead Hill), attempts were made to study the formation of a footpath socies, by observations carried out on several areas where the footpath was diverted to fresh ground. Permanent quadrats were unfortunately obliterated, but the following facts were revealed from close observation.

Existing species not typical of the footpath synusia were suppressed and bare ground populated by Poa pratensis which in some cases sprang from seed, but in others proliferated from pre-existing individuals. Plantago spp also appeared as seedlings upon this central area and grew to maturity. Lolium perenne did not appear as seedlings in the first place, but pre-existing specimen persisted and proliferated, and in the second year seedlings were observed.

Trifolium repens invaded the outer margins of the path vegetatively. The runners appeared to be attracted towards the unshaded area from individuals existing in the surrounds. This character of Trifolium repens is discussed later in this work. Runners of Trifolium repens were defoliated by the action of treading and were pressed into the puddled ground, but in many cases recuperated.

THE VEGETATION OF FLAGGED FOOTPATHS

Several types of flagged pavements are in existence, the commonest being the ordinary sidewalk of the roadside. In this case the flags may be of stone or concrete, but in both cases interstices exist between the flags. Garden paths and field paths are sometimes flagged and even asphalt paths possess a kerb which is composed of individual stones. Cobbled paths and roadways are of uncommon occurrence at the present time.

Except in the centre of large cities or in the presence of chemical fumes or similar agents destructive to plant life, all flagged pavements possess vegetation, though this is in many cases extremely scanty. Lower forms of plant life such as mosses and algae may cover the flags or exist in the interstices, but their distribution is not considered in this work.

The complete floristic list of the habitat is indefinitely large and ranges from seedling trees to grasses, but the frequency of the majority is of so low an order as to be negligible. They are accidentals, occurring in odd sheltered or protected places.

The remarkable character of the vegetation of this type of habitat is the dominance of Poa pratensis over all other species. This species occupies the interstices between the flags, sometimes dominating this area and sometimes occurring in scattered colonies. It is practically constant for all examples occurring on flagged pavements in the most varied localities.

Sub-Dominant species are Galium spp and Sagina procumbens.

Where the flagged path borders a bank or wayside the latter situations may be populated by a large variety of species, yet Poa pratensis still dominates all the interstices of the flags. Table V gives an example of this phenomenon. (This table was published in a previous paper in 1929,(12), and is reproduced below.)

TABLE V

Flagged Footpaths and Sidewalks

Average of 20 Cases

Margin of Path	per cent. area	Interstices of Flags.	per cent area
Bent. Agrostis ssp.	35.	Smooth stalked Meadowgrass (Poa pratensis)	*95
Wooly Softgrass (Holcus mollis)	15		
Sheep's Fescue (Festuca ovina)	25	Miscellaneous	*5
Couch or Twitch (Agropyrum repens)	5		
Wild White Clover (Trifolium repens)	5	* Not including bare ground, area covered by vegetation only considered.	
Smooth stalked Meadow-grass (Poa pratensis)	5		
Annual Meadow-grass (Poa annua)	5		
Miscellaneous	5		
	100		100

There appear to be two reasons for the dominance of this particular plant, firstly the ability to invade the interstices by means of its runners, and secondly the adaptation to resist the injury brought about by the very severe and concentrated treading. This power of resistance is due to life form and leaf and stem structure and has already been fully described in the case of the ordinary grass footpath.

In the case of disused flagged paths or those rarely trodden, the flora may be extremely varied and possess no distinct characters, this also applies with cobbled paths.

The colonisation of a newly laid flagged path takes place by seed infection of the soil of the interstices and by invasion from the surrounds by runner bearing species. The commonest ubiquitous annuals may appear together with Agrostis or Agropyrum. Poa pratensis may appear as isolated seedlings in the interstices or from runners invading from the surrounds. The mechanical effect of treading soon exerts its selective influence, Poa pratensis surviving on the closely trodden portions.

Fig.24 shows the domination of an interstice by Poa pratensis while the immediate surrounds (Fig.25) contain a mixed flora. Fig.26 shows a flat topped flagged wall lying flush with a field on one side and a bank top on the other, this exactly resembles a flagged path in structure. An iron rail fence protects this wall top from treading and it will be seen that a flora similar to that of the field has invaded the interstices and persisted.

Conclusions

The chief factor concerned in the production of the footpath socies from the grassland community is the mechanical influence of treading and puddling. This exerts a selective influence on the gramineous species eliminating those not structurally adapted to withstand the injury of treading and puddling. The species adapted by virtue of life form and leaf and stem structure are able to persist. These dominants are arranged in zonation according to the intensity of treading. Under dry conditions where no puddling occurs, treading alone produces little change.

Plantago spp are governed by the same factor as the gramineous species and owe their existence to their life form. Trifolium repens does not exhibit as great a resistance to treading as do the gramineous species and occupies the outer zone in consequence of this. Light appears to be the influencing factor with this species, shading being eliminated by the treading of tall species.

* The prostrate rosette habit of growth of the footpath dominants appears to be due to the consolidated condition of the ground apart from the action of treading.

The interstices of flagged paths and sidewalks are dominated by Poa pratensis. This is owing to the ability of this species to invade the area by means of runners coupled with its structural adaptations to resist injury by treading.

* This matter is fully discussed in Section 10.

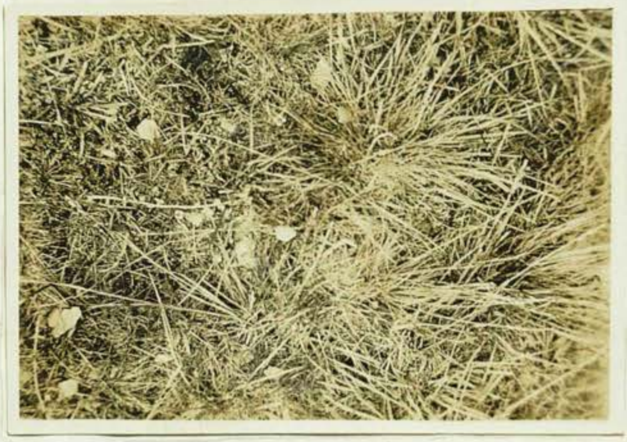
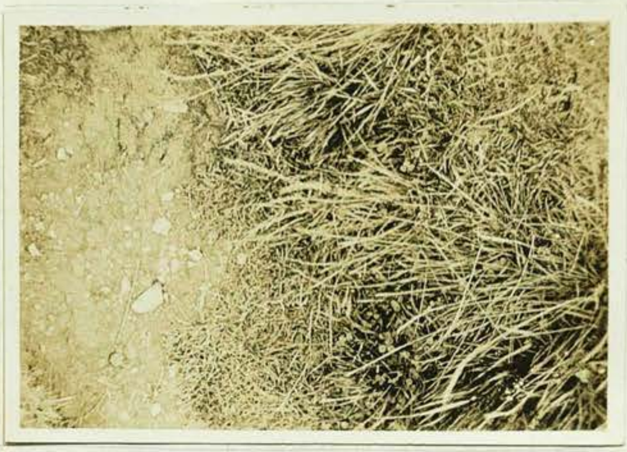


Fig.1. Type of herbage adjoining footpath.
Tarn Howes,Lake District).



A. B. C. D.

Fig.2. Vegetati0n of footpath illustrating zonation.
A. Bare ground.
B. Poa pratensis.
C. Trifolium repens.
D. Lolium perenne.
(Tarn Howes,Lake District).

Fig.3. Vegetation of dry sandy heath.(S.Wooton,Norfolk).

A B

Fig.4. Vegetation of footpath on dry sandy heath. (S.Wooton,Norfolk).
A.Agrostis-festuca zone.
B.Agrostis-holcus zone.

Fig.5. Life form of Dactylis glomerata.Note position of growing points of shoots below ground level,or at the surface.

(a)

(b)

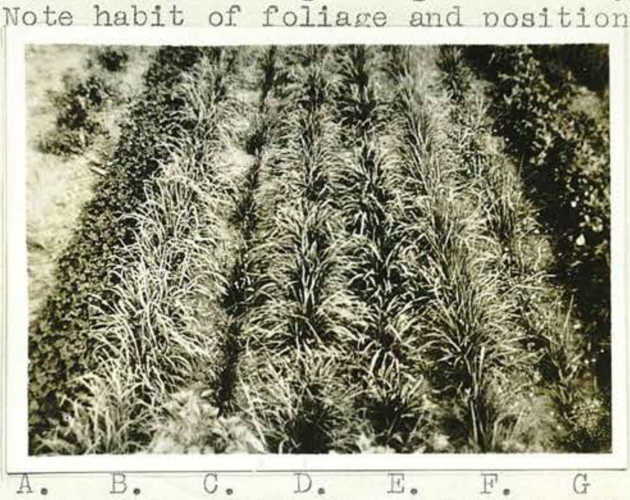
Fig.6. Life forms of (a) Poa pratensis.and (b) Lolium perenne.
Note position of growing points of shoots below ground level, at a lower level than those in figs. 5,above.

A B C

Fig.7. Life forms of (a) Festuca elatior.(b) Agrostis stolonifera.(c) Agropyrum repens. Note position of growing points of shoots at or above ground level. Note also aerial shoots of (b) Agrostis stolonifera.

A B C

Fig.8. Variation of life form in response to habitat (habitat forms) of Plantago major.
(a) Plant growing on loose soil.
(b) & (c) Plants growing on heavily trodden ground
Note habit of foliage and position of growing point



A. B. C. D. E. F. G

Fig.9. Experimental strip of individual species (a) Trifolium repens.(b) Dactylis glomerata.(c) Poa pratensis.(d) Lolium perenne.(e) Festuca elatior (f) Agrostis stolonifera. (g) Agropyrum repens.

Fig.10. Duplicate experimental strips of individual species (a) Trifolium repens.(b) Dactylis glomerata (c) Poa pratensis.(d) Lolium perenne (e) Festuca elatior.(f) Agrostis stolonifera (g) Agropyrum repens.(This species was a partial failure in this plot).

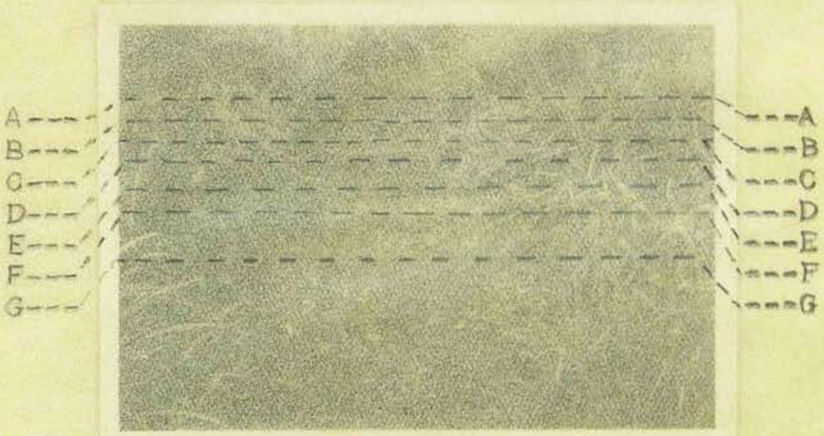


Fig.11.Footpath cut through experimental plot 1.and treading in progress during damp condition of soil.
(a) Trifolium repens.(b) Dactylis glomerata.(c)Poa pratensis.(d) Lolium perenne.(e) Festuca elatior.(f) Agrostis stolonifera.(g) Agropyrum repens.

Fig.12.Side view of fig.11 above.
(a) Trifolium repens (b) Dactylis glomerata.(c) Poa pratensis.(d) Lolium perenne.(e) Festuca elatior.(f) Agrostis stolonifera.

A B C D E F G

A

G

B C D E F

Fig.10. Duplicate experimental strips of individual species (a) Trifolium repens.(b) Dactylis glomerata (c) Poa pratensis.(d) Lolium perenne (e) Festuca elatior.(f) Agrostis stolonifera (g) Agropyrum repens.(This species was a partial failure in this plot).

A--- B--- C--- D--- E--- F--- G---

---A ---B ---C ---D ---E ---F ---G

Fig.11.Footpath cut through experimental plot 1.and treading in progress during damp condition of soil.
(a) Trifolium repens.(b) Dactylis glomerata.(c)Poa pratensis.(d) Lolium perenne.(e) Festuca elatior.(f) Agrostis stolonifera.(g) Agropyrum repens.

A B C D E F

F

A B C D E

Fig.12.Side view of fig.11 above.
(a) Trifolium repens (b) Dactylis glomerata.(c) Poa pratensis.(d) Lolium perenne.(e) Festuca elatior.(f) Agrosti stolonifera.

D E F G

Fig.13. Continuation of Fig.12 above.(D.E.&.F. overlapping).
(D) Lolium perenne.
(E) Festuca elatior.
(F) Agrostis stolonifera
(G) Agropyrum repens.

A B C D E F G

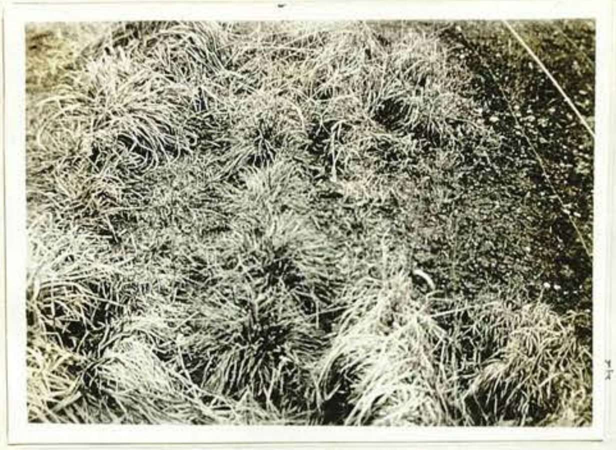


Fig.14. Side view of footpath cut through duplicate experimental plot.2. showing grasses after a fortnight rest from treading.

(A) Trifolium repens. (B) Dactylis glomerata. (C) Poa pratensis (D) Lolium perenne.(E) Festuca elatior (F) Agrostis stolonifera.(G)Agropyrum repens (This species practically failed.

A B

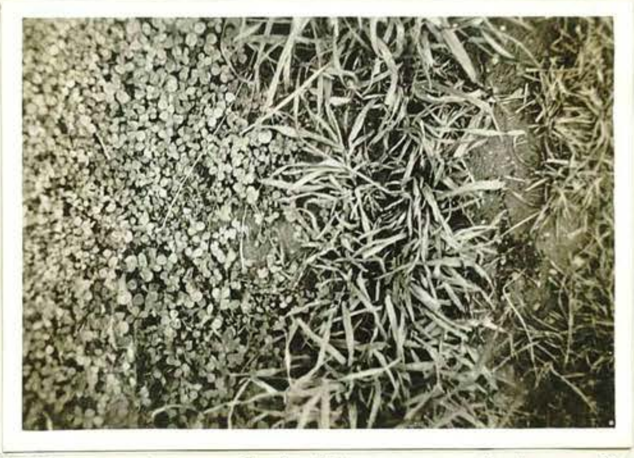


Fig.15.Close view of influence of treading upon the individual species (after a fortnight resting period to allow for possible recovery) Experimental plot 1. (a) Trifolium repens.(b) Dactylis glomerata.

C D

Fig.16.Continuation of Fig.15.
(c) Poa pratensis
(d) Lolium perenne.

D E

Fig.17.Continuation of Fig.16 (with D.overlapping)
(D) Lolium perenne.
(E) Festuca elatior (note dead or bruised condition of centre of tufts)

F. G.

F G.

Fig.18.Continuation of Fig.17
(F) Agrostis stolonifera (note dead condition)
(G) Agropyrum repens (note that this species is dead and almost obliterated.)

A B

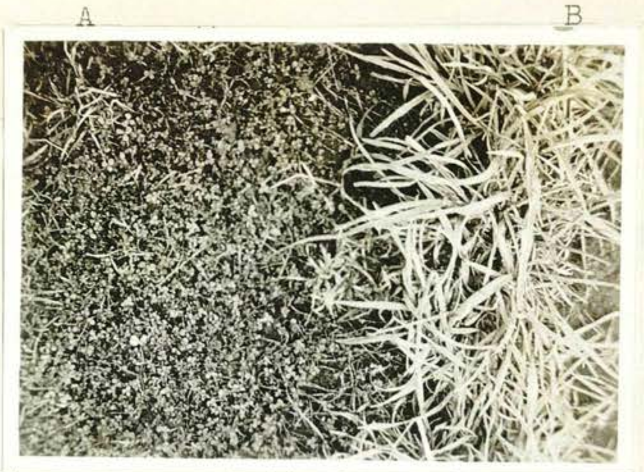


Fig.19. (Duplicate plot) Close view of influence of treading upon the individual species (after a fortnight resting period to allow for possible recovery Duplicate experimental plot.2.
(A) Trifolium repens.
(B) Dactylis glomerata.

C

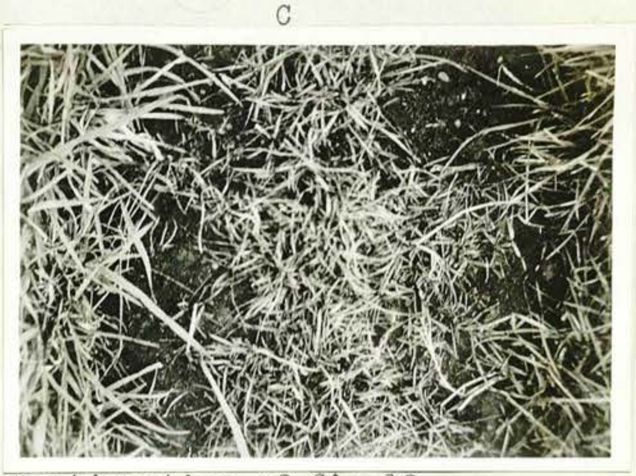
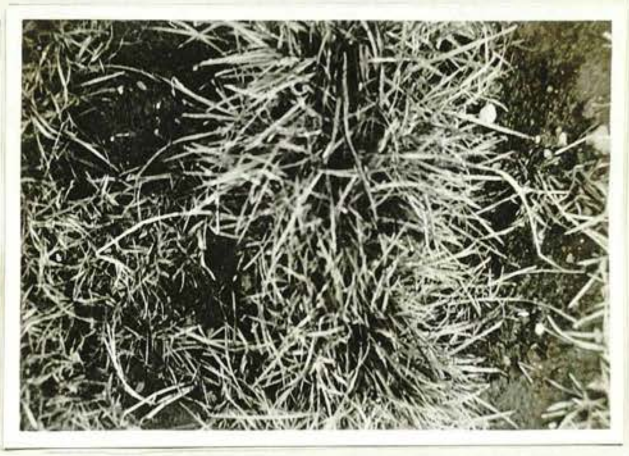


Fig.20. Continuation of fig.19.
(C) Poa pratensis.

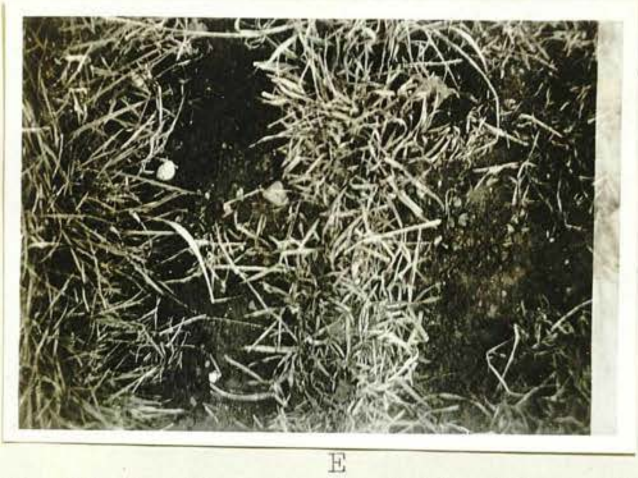
D



D

Fig.21. Continuation of fig.20.
(D) Lolium perenne.

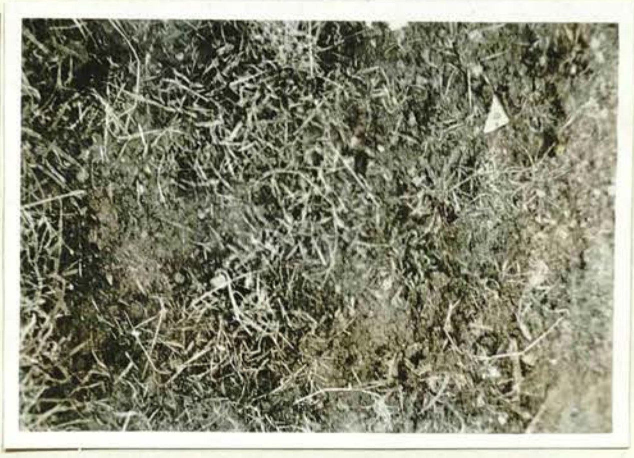
E



E

Fig.22.Continuation of fig.21. (E) Festuca elatior (note dead or bruised condition of centre of tufts.)

F G



F G

Fig.23. Continuation of fig.22. (F) Agrostis stolonifera (note almost obliterated condition) (G) Agropyrum repens (traces of the dead remains may still be seen. This species was a failure on this strip.

A.

B.

Fig. 23. A & B. shewing selective lethal effect of "Rubber Rejuvenator" (see Sec 22) upon Agrostis & Holcus spp. Photographs taken three weeks after treatment.

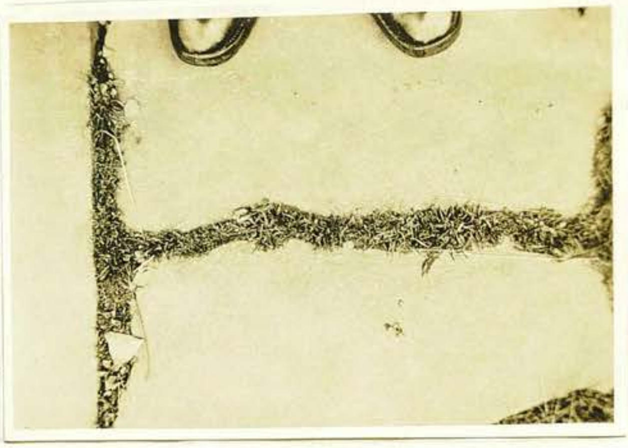
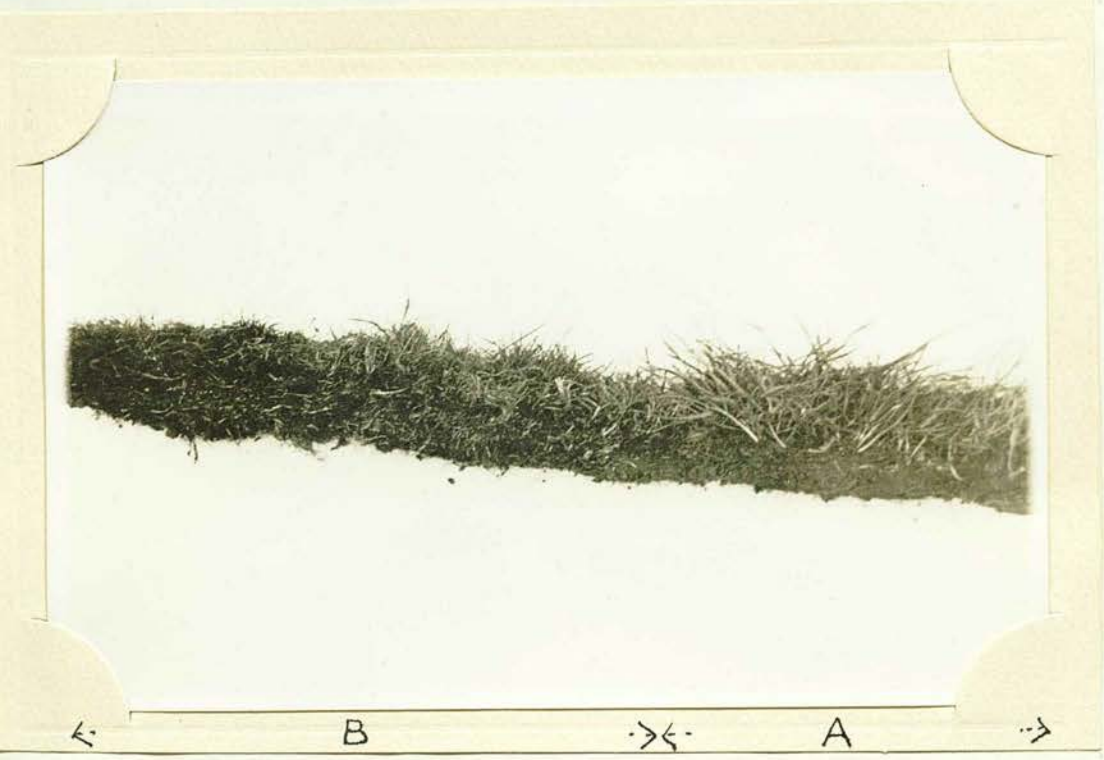


Fig.24. Interstices of flagged footpath dominated by Poa pratensis. (Hawkshead Hill.Lake District).

Fig.25. Margin of flagged footpath (fig 24 above) The margin is populated by Agrostis stolonifera. Festuca ovina Ranunculus spp and Circaea lutetiana.

Fig.26. Interstices of flags where treading does not occur The interstices are populated by Trifolium repens, Lolium perenne,Agrostis stolonifera.(Hawkshead Lake District.)



Section of portion of a footpath (A) and surrounds (B) (Hampsfell. Grange-over-Sands, Lancs). Note the deep seated perennating buds of Poa pratensis and Lolium perenne on the footpath (A) and the comparatively solid appearance of the soil. The surrounds (B) are composed of an association of Agrostis spp Festuca spp and Luzula spp. The growing points are situated above the soil level, and resting upon a mat of dead and living root material.

SECTION.

4

THE VEGETATION OF CART-TRACKS AND GATEWAYS

THE VEGETATION OF CART-TRACKS AND GATEWAYS

THE VEGETATION OF CART-TRACKS AND GATEWAYS

Cart tracks and gateways possess a characteristic vegetation, the chief features of which are constant for all parts of the British Isles.

Deeply rutted lanes and regions churned and puddled by cart wheels and horse's hoofs cover a large area of the country side, probably of greater magnitude than that occupied by footpaths. In certain cases the disturbance due to transport is only partial, e.g. in rutted lanes when the ground between the ruts is undisturbed, but even in these examples the disturbance often alters its direction, so that undamaged areas are not permanently immune from interference.

In certain cases transport during wet weather is so heavy that the whole surface becomes churned into a morass. Examples of this kind may be seen in fen droves. Fig.27. The latter type of cart track provides an excellent subject for study of this kind of vegetation. Transport, mainly of farm produce, is carried out during the autumn and winter months and the puddling becomes so severe that fresh areas have to be chosen. This accounts for the great width of the fen droves.

Gateways exhibit a vegetation of similar features to that of cart tracks, except that the outer fringe or ecotone of the area varies with regard to species and zonation, according to whether the field entered is under grass or arable cropping.

The following are the chief species on cart-tracks and gateways:- Plantago major, Polygonum aviculare, Matricaria suaveolens, Senebiera Coronopus, Potentilla anserina, Poa pratensis. In the case where the gateway merges into a grass field, the species of this ecotone are those of the footpath and exhibit the same arrangement as regards zonation. In the case of a little used but rutted cart track the vegetation of the raised area between the ruts may be that of a grassland community.

For the purpose of this section, the areas chosen for study are the definitely disturbed areas. Regions which escape this influence, such as the space between the ruts on a little used track or the ecotone where a gateway area merges into a grass field, are not investigated. In the latter case the vegetation of the ecotone is the same as that of the footpath. It exhibits the same zonation owing to similar influences to those at work upon the footpath, i.e. compression and disturbance which is of the same degree of intensity as that upon the footpath and much less severe than that inflicted upon the areas nearer the gate.

For the above reasons the areas chosen for study are fen droves or un-metalled roads, and gateways leading into arable fields.

Table VI gives quantitative data regarding the species of these areas and Table VII the qualitative data.

T A B L E   VI

S P E C I E S	Fen Drove Example I			Cart Track Example II			Cart Track Example III			Gateway Example IV			Gateway Example V		
	Abundance %	Frequency %	Areal %	Abundance %	Frequency %	Areal %	Abundance %	Frequency. %	Areal %	Abundance %	Frequency %	Areal %	Abundance %	Frequency %	Areal %
Plantago major	12	19	7	19	100	28	12	80	18	11	100	20	14	18	8
Polygonum aviculare	21	83	27	21	100	20	18	41	10	27	100	16	17	30	12
Matricaria suaveolens	22	61	8	21	100	18	25	51	7	22	100	17	20	39	9
Senebiera Coronopus	16	40	7	18	100	12	8	57	10	17	100	22	11	17	9
Potentilla anserina	10	15	14	0	0	0	10	8	13	0	0	0	7	30	18
Poa pratensis	12	72	15	12	70	12	17	63	7	18	100	18	16	90	10
Agrostis spp	4	10	6	5	18	4	4	8	2	3	10	5	12	39	12
Miscellaneus	3	28	6	4	18	2	6	16	5	2	8	2	3	10	2
BARE GROUND	-	8	10	-	10	4	-	25	28	-	0	0	-	20	20
	100	-	100	100	-	100	100	-	100	100	-	100	100	-	100

TABLE VII

AVERAGE OF 100 EXAMPLES

SPECIES	Constancy	Exclusiveness	Sociability	Vitality	Periodicity
Plantago major	100	3	1-2-3-4	●	v ae au
Polygonum aviculare	92	3	1-2-3-4-5	●	*v ae au
Matricaria suaveolens	89	3	1-2-3-4-5	●	*v ae au
Senebiera Coronopus	79	3	1-2	●	v ae au
Potentilla anserina	60	3	2-3-4-5	●	v ae au
Poa pratensis	94	2	1-2-3	●	w v ae au
Agrostis spp	54	2	2-3-4	⊖	v ae au
Miscellaneous	100	1	1-2-3-4-5	○	w v ae au

For meaning of figures under each heading see {Section 1 page 16. Section 3 Table II

*late spring

Belt and line transects illustrating zonation and arrangement of species are not used in this section as photography is again possible and gives an accurate picture of conditions.

It will be seen from the above tables that there is no correlation between areal percentage of ground covered, frequency or abundance. The size of the individuals varies enormously as does the area covered and the abundance. Frequence does not vary to the same extent and exhibits a certain amount of similarity in the case of individual species in each example. This latter phenomenon is due to a certain amount of zonation of the species.

There is one outstanding phenomenon which is observed as being constant for all examples, i.e. that perennials do not exist upon the areas which are disturbed and puddled in winter, except in a seedling or "maiden" state. These areas are dominated by the annuals Matricaria suaveolens and Polygonum aviculare and in some cases by seedlings and immature plants of Plantago major.

Despite the great variation in the size and arrangement of the species the characteristic floristic composition of gateways and cart tracks remains constant for all parts of the country.

Figs. 27, 28, 29, give an illustration of the winter, vernal and late aestival or autumnal aspects of a fen drove.

HABITAT FACTORS

The habitat of the communities under consideration bears some features of resemblance to that of the footpath, in that it is a disturbed area, and the disturbance is due to puddling. In this case, however, the disturbance is of a much more violent nature, the soil being puddled and stirred to depths of several inches, or in the case of cart ruts often to the depth of the axles. Certain parts of the area are disturbed during winter months when the ground is soft, other parts as for example the region between the cart wheels and the horse's hoofs remain undisturbed. During summer the ground becomes hard, and though still subjected to pressure, comparatively or quite stable.

Edaphic Factors

Owing to the fact that the gateway and footpath communities are constant for all types of soil, the chemical composition of the soil and to a certain extent its physical condition, i.e. humus, clay, sand or chalk content, cannot have any definite influence upon the flora. On sandy heaths (Bawsey and Snettisham, Norfolk, Greensand formation) the same flora is found as upon heavy clays.

On soils containing a clay fraction, "poaching" and deflocculation of the clay particles occurs, but this is not the case on sands.

+The consolidated condition of the soil produces the prostrate habit as was the case upon footpaths.

Light

The habitat is fully illuminated as was the footpath, owing to the absence of other vegetation.

+ See Section 10.

There appears to be some connection between the light factor and the vegetation as all the species with the exception of Matricaria suaveolens are prostrate or straggling, and are unable to compete for light in other habitats. Matricaria suaveolens is a composite with dissected leaves, and it is well known that species of that order and with that type of foliage are extremely intolerant of shade.

In the above connection observations were made in several localities with regard to the reaction of Matricaria suaveolens to light. The first three examples were those of cart roads running E-W. Where the hedge was dense and the ground overshadowed by it or by trees, Matricaria suaveolens was absent or scanty. On the illuminated areas it grew abundantly. In the case of a Marshland drove (Walpole X keys), shaded by Poplar trees, the species was absent, but occurred at the end of the drove where the trees ceased. In the case of gateways, if any part of the habitat was overshadowed by trees the species was absent or scanty. One example occurred (Castle Rising, Norfolk) where the shadow from a building shaded the sidewalk up to the inner edge of the kerb, a little Matricaria suaveolens grew under the wall and on the sidewalk, but it was abundant upon the kerb. Figs. 30,31,32 & 33, illustrate the influence of aspect upon the species.

It is a significant fact that Matricaria suaveolens, Senebiera Coronopus and Polygonum aviculare, all germinate comparatively late when other regions are overshadowed by vegetation. Seedlings of these species are not to be observed on cart tracks or gateways until the end of May. It appears probable that the latter habitats are the only ones offering light and a suitable situation for germination at this season.

From the above observations it appears that light is a contributing factor to the existence of the community

THE INFLUENCE OF DISTURBANCE AND COMPRESSION

It is obvious that the chief factor influencing the habitat is that of disturbance of the ground during winter and compression of the surface in summer when the ground is dry.

The effect of the winter disturbance is to destroy all species which have become established during summer. These species consist of the annuals Polygonum aviculare, Matricaria suaveolens, Senebiera Coronopus, and the seedlings and ~~coming~~ first year plants of Plantago spp together with a few miscellaneous seedling perennials. The annuals would obviously die irrespective of the disturbance, but the perennials are also destroyed. Observation shows that runner bearing perennials are crushed beneath the wet soil while Plantago major is squeezed out, and left upon the surface to be destroyed by frost or other agencies.

It is to be observed in any of these communities that the perennials of more than one years standing are found on parts of the habitat which are stable during winter. Figs. 34, 35, illustrate this point. Figs. 36, & 37, shew the contrast between the species of a stable area and those of the adjoining unstable area.

Potentilla anserina, having its main rootstocks established upon stable undisturbed ground, may during summer send runners over an area which was disturbed during winter. It does not however tolerate much treading. Fig.38, shews Potentilla anserina colonising an undisturbed area between the cart tracks in a fen drove.

Robinson (41, and private communication) reports that when ducks were penned on a grass sward, the grass was destroyed and an associes was produced which was composed of Plantago major, Matricaria suaveolens and later Polygonum aviculare.

This case offers an excellent substantiation of the contentions expounded above. Ducks subject the ground to severe puddling, without any deep disturbance such as that occasioned by wheels or horse's feet.

After removal of the ducks the grasses reasserted themselves (See also Sec 10. page 180.)

THE STRUCTURAL RESISTANCE TO TREADING

The species Plantago major, Matricaria suaveolens, Polygonum aviculare, Senebiera Coronopus and Poa pratensis are all resistant to treading. The resistance of Poa pratensis and Plantago major in virtue of their life form and structure has already been discussed and illustrated in Figs. 6 & 8, Section 3. The remaining species are also adapted to this influence.

Polygonum aviculare has hard wiry stems which resist treading and the plant is present in prostrate form which prevents snapping of the stem at any certain point. The leaves are small and become much smaller when the plant is subjected to treading. (This latter phenomenon is fully discussed in section 8 which deals with a similar phenomenon in the case of Trifolium repens) The flowers are minute and are protected in the axils of the leaves.

Senebiera Coronopus is prostrate, has small scale like leaves and small flowers and thus survives compression.

*Matricaria suaveolens is normally an upright plant but can become prostrate. The ability of this plant to resist treading appears to be due to the small area of finely dissected leaves, and the extremely pliable nature of the stem which is tough and fibrous and does not snap if bent double. The flower heads are comparatively large, but if compressed they splay out and appear to escape injury.

It must be made clear that the species of the community do not flourish under compression but are severely stunted in growth both with regard to shoot and root system.

* The widespread distribution of M. suaveolens on the sites mentioned above, is interesting as it is of recent introduction. It is often confused with M. inodora by casual observation.
The latter species does not tolerate treading like M. suaveolens, and when the two species occur together in the neighbourhood of a cart track or gateway, there is a distinct separation into zones in relation to treading. See Fig 31. A.
M. suaveolens is actually becoming a troublesome weed on the margins of fields and waste places in W. Norfolk.

They are also altered as regards habit, being converted from the upright or semi upright to the prostrate habit. Figs. 39-42, shew the contrast between individuals of the species Polygonum aviculare, Matricaria suaveolens, and Senebiera Coronopus grown in loose and untrodden ground with those grown on solid trodden areas. (cf with Fig.8 Section 3. Plantago major) While the species are severely suppressed, they are, however, capable of completing their life cycle.

Conclusions

The characteristic flora of a cart-track or gateway community, owes its existence to a peculiar combination of circumstances.

Severe disturbance and churning of the ground in winter exterminates all perennial species which have seeded during summer, annuals dying naturally or by this disturbance.

During summer the disturbed area becomes hard and stable, but is still subjected to surface pressure, and is therefore populated by annuals and seedling perennials, (the latter being chiefly Plantago major & Poa pratensis). These are, in virtue of their life form and habit, enabled to resist the injury of treading to a sufficient degree to continue their existence through the summer and autumn. Other species than the above may appear during spring and summer as accidentals, but succumb to treading.

The undisturbed areas between or around the disturbed region are populated by perennials which may resist treading to a severe degree, but cannot survive severe disturbance and churning of the ground during winter.

All the species are ill adapted to compete for light and the habitat offers illumination without competition. It also favours species which germinate comparatively late in spring.

Fig.27. Fen Drove. Winter aspect. (Hilgay Fen).

Fig.28. Fen Drave. Vernal aspect.(Hilgay Fen).

Fig.29. Fen drove.Aestival-autumnal aspect.(late August)
Hilgay Fen). The dominant species is Polygonum aviculare.

Fig.30. Shaded side of roadway.Matricaria suaveolens absent. (Clipstone,Norfolk).

Fig.31. Unshaded side of roadway (above) Matricaria suaveolens present. (Clipstone Norfolk.)

Fig 31.A. Shewing zonation of Matricaria inodora in relation to treading. Untrodden area on right is dominated by M. inodora while the area on the left is trodden and M. suaveolens is present, note shorter herbage on left.

Fig.32. Unshaded side of gateway.Matricaria suaveolens present. (Terrington St.Clements.Norfolk).

Fig.33. Shaded side of gateway (above) Matricaria suaveolens absent.(Terrington St.Clements,Norfolk).

Fig.34. Perennial species occupying untrodden and undisturbed areas.(Fen drove Hilgay Fen).

Fig.35. Perennial species occupying untrodden and undisturbed areas.(Fen Drove Hilgay Fen).

Fig.36. Perennial species. Agrostis spp. Agropyrum repens. Plantago major and Potentilla anserina occupying stable margins. Poa annua and seedlings of Matricaria suaveolens occupying disturbed region. (Fen drove, Northdelph, Downham Market).

Fig.37. Perennial species Dactylis glomerata and Plantago major occupying stable margin. Seedlings of Matricaria suaveolens and Polygonum aviculare, occupying disturbed region. (Fen drove Northdelph Downham Market).

Fig.38. Potentilla anserina and Plantago major dominating undisturbed region between cart tracks. (Fen drove Hilgay Fen).

A B

Fig.39. (A) Senebiera Coronopus from untrodden ground.
(B) The same species from trodden ground.

A B

Fig.40. (A) Matricaria suaveolens from untrodden ground
(B) The same species from trodden ground.

Fig.41. Polygonum aviculare from untrodden ground.

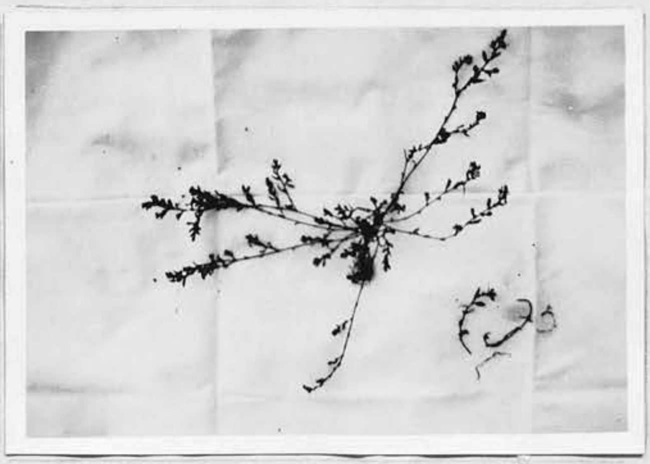


Fig.42. Polygonum aviculare from trodden ground (cf
fig.41.above)

SECTION.

5.

THE VEGETATION OF WAYSIDE AND HEDGEROW

THE VEGETATION OF WAYSIDE AND HEDGEROW.

Tuesday Afternoon—
King's Lynn Corn Hall, Stand 34.

TELEPHONE: KING'S LYNN 547.

Norfolk County Council.

DEPARTMENT OF AGRICULTURAL EDUCATION.
(*West Norfolk Office.*)

THE NORFOLK COUNTY COUNCIL

NATIONAL SCHEME FOR DISABLED MEN

F. RAYNS, M.A.
DIRECTOR OF AGRICULTURAL EDUCATION

G. H. BATES, D.SC.
SENIOR AGRICULTURAL ADVISER.

ST. JAMES HOUSE,
KING'S LYNN.

Please quote in reply:—K.L.
Your Reference:—

Oct. 6th. 1934.

Professor A.G. Tansley. F.R.S.
Grantchester.
Cambridge.

Dear Sir.

I am writing to you with reference to the publication of a thesis entitled "Semi-Natural Vegetation and the Biotic Factor" which is entirely of an ecological nature, and for which I received the degree of D.Sc. of the University of Edinburgh.

Several of the subsidiary papers of this thesis have been published, but the main part of the work, dealing with the ecology of footpaths, cart tracks, waysides etc and with the autecology of C. arvense have not been published.

Proff Sir Thomas Hudson-Beare has urged me to have the work published, and Dr W.B. Turrill of Kew who has seen part of the work on C. arvense suggests that I should write that up for the "Journal of Ecology". I communicated my work on the autecology of Urtica dioica to the British Ecological Society last January, and published a paper in the "Journal of Ecology" Vol. XXII. No 1.

Tuesday Afternoon—
King's Lynn Corn Hall, Stand 3…

TELEPHONE: KING'S LYNN 547.

Norfolk County Council.

DEPARTMENT OF AGRICULTURAL EDUCATION.

(*West Norfolk Office.*)

ST. JAMES HOUSE,
KING'S LYNN.

F. RAYNS, M.A.
DIRECTOR OF AGRICULTURAL EDUCATION
G. H. BATES, D.SC.
SENIOR AGRICULTURAL ADVISER.

Please quote in reply:—K.L.
Your Reference:—

I had it in mind to publish all the work relevant to semi-natural vegetation as a small book or to offer it for publication to the "Journal of Ecology".

If I forward the work to you, would you be so good as to give me your advice on the matter?

Thanking you for past help.

Yours truly.
G. H. Bates.

45-74 Footpaths + Sidewalks
74-81 Cart tracks + Gateways

93-106 Waysides + Hedgerows

7-122 Creeping Thistle. Could only publish short summary of 2 or 3 pages 1000-1500 words

THE VEGETATION OF WAYSIDE AND HEDGEROW.

"Wayside" is the term used to define the area which lies between the roadway and the hedge, wall or fence, which separates this ground from the fields. In the case of common land there is often no boundary fence of any description, and the wayside becomes an arbitrary region. In some cases there is a steep bank falling to the road and here no wayside region exists, in the strict meaning of the word, for the bank or hedgerow possesses certain distinct features.

The hedgerow is that area which is constituted by the actual hedge itself, and the bank upon which it stands, except where it is planted upon level ground as it is in some cases. The hedge, whether upon a bank or on the level, is associated with a definite type of vegetation.

It will be seen that it is impossible to draw a sharp distinction between the wayside and hedgerow regions and for this reason they are considered as one unit.

As already stated, the wayside passes through every type of country, and is consequently influenced to a certain extent by the factors which have produced the vegetation of that country, and it is also in some cases subject to invasion by species from the surrounding land. This latter phenomenon is illustrated in Figs. 43 and 44.

In spite of the above influences the wayside possesses a type of vegetation which, in its main characters, has a remarkable constancy for all parts of the country, with a few differences due to climatic or other factors.

The most striking feature of wayside and hedgerow is the arrangement of species into consocies, socies, and colonies running in zones parallel to the roadway. This arrangement is most notable when the species are in flower. A seasonal succession takes place in certain zones while others show no variation throughout the whole year.

Floristic Composition and Arrangement.

Commencing with the edge of the roadway, the vegetation of the "gutter" region is often similar to that of the gateway and cart track, possessing the same dominant species in the same arrangement (Fig. 45). This is succeeded or replaced by the flora of the footpath with a similar zonation, if the margin of the wayside is trodden. (Fig 46) Where treading does not occur, it is usual to find Agrostis, spp, Festuca spp or Dactylis (Fig. 47). Where the margin is raised above the level of the road, and is dry in consequence, Festuca is the dominant species. A footpath may occur on any part of the wayside, and with it the footpath community.

The middle region of the wayside is usually dominated by Dactylis glomerata or Holcus lanatus, though this and the marginal region are often covered to a certain extent by sand and gravel heaps which are colonised by any of the following, Cirsium arvense, Urtica dioica, Agropyrum repens, or by Potentilla anserina (See Sections 6 and 7). The most frequent colonist of these heaps is Cirsium arvense. At a point about the junction of the middle and outer region a colony of Leontodon autumnalis often exists in the form of a zone, during autumn. Fig. 48.

The inner region of the wayside often merges into that of the hedge bank, and thus no distinction can be drawn between these areas. They must often be considered as one. The vegetation here consists of Arrhenatherum avenaceum, Bromus spp, Holcus mollis, Festuca ovina, Agrostis spp, Agropyrum repens and Hordeum murinum as the dominant gramineous species Urtica dioica is almost constant, as is Galium Aparine. Of the umbelliferous species, Anthriscus sylvestris dominantes the vernal aspect. Daucus carota and Peucedanum sativum are often dominants and Smyrnium Olusatrum on the coast.

The season for Anthriscus is short, and it is followed by a zone of Arrhenatherum with Heracleum Sphondylium. Aegopodium Podagraria frequently dominates the hedge bank over small areas in the immediate neighbourhood of gardens. Malva, spp, are sometimes common.

The hedge itself dominates the top of the bank and is usually of Crataegus Oxyacantha, but other species are employed for this purpose, e.g. Ulmus campestris, Fraxinus excelsior, Fagus sylvatica, Corylus Avellana, Ilex Aquifolium Acer campestre, Cornus sanguinea. In certain parts of East Anglia coniferous species are employed (Figs. 101-104 49-57). Occasionally Ligustrum vulgare is used.

Many species are present on the wayside and hedgerow as sub-dominants and casuals and as already stated, a complete floristic list would comprise almost the entire British flora.

The floristic composition and analytical data of waysides and hedgerows are set out in Tables VIII, IX, X, XI. The wayside was taken as the region between the roadway and the foot of the hedge bank. The hedgerow data were chosen from hedgerows where there was no wayside, i.e. where the bank rose straight from the roadway or sidewalk or from hedgerows

occuring

TABLE VIII WAYSIDES

IO EXAMPLES

DATE	16-7-32		20-7-32		21-7-32		10-9-32		3-9-32		8-6-32		18-9-32		18-7-32		18-9-32		17-7-32	
	EX.I		EX.II		EX.III		EX.IV.		EX.V.		EX.VI.		EX.VII.		EX.VIII		EX.IX		EX.X.	
SPECIES	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %	Frequence %	Areal %
Poa pratensis	12	16	5	5	8	7	12	8	12	5	12	1	10	5						
Lolium perenne	12	4	15	7			37	25	20	10	20	12					37	17	12	5
Dactylis glomerata	27	15	27	10	58	32	56	40	31	27	55	20			70	25	21	10	17	10
Agrostis spp			7	2	38	16			22	14			80	35	75	25	50	18		
Festuca spp					30	10							63	23	80	15	56	5		
Agropyrum repens	27	25	52	20															7	1
Holcus lanatus					22	15	7	5	20	8	21	10					16	7	30	10
Bromus spp																			42	25
Arrhenatherum avenaceum	30	18	7	5	25	20	10	10	25	20			23	10			12	10		
Hordeum murinum											2	1								

Matricaria [illegible]																				
Cirsium arvense			3	1							6	2							22	5
Cirsium lanceolatum											4	1							7	1
Urtica dioica	12	6	60	50							32	19								
Aegopodium Podagraria											1	5								
Plantago major	4	2									8	5								
Plantago media													8	6						
Plantago lanceolata													19	4			100	15		
Polygonum aviculare	16	6									5	3							12	2
Anthemis Cotula											2	3								
Senebiera Coronopus											2	4							7	2
Trifolium repens									15	8					25	10			4	1
Papaver Rhoeas	1	-									3	5							31	18
Ranunculus spp	16	7															34	15		
Leontodon autumnalis							12	4	7	3			16	5			4	3		
Lamium album																				
Rumex obtusifolius		1																		
Nepeta hederacea															1	5				
Capsella Bursa-pastoris																			29	15
Pteris aquilina															15	20				
Miscellaneous	5	-	8	-	7	-	10	-	5	-	9	-	17	-	4	-	8	-	18	-
Total	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100	-	100

* Traces of Trifolium repens were found in Examples I. II. III. IV. VI. VII. & IX.

TABLE IX

AVERAGE OF IOO EXAMPLES

SPECIES	Constancy	Exclusiveness	Sociability	Vitality	Periodicity
Poa pratensis	94	3	2-3-4	●	v ae au w
Lolium perenne	89	3	2-3-4-5	●	v ae au w
Dactylis glomerata	97	3	2-3-4	●	v ae au
Agrostis spp	83	2	2-3-4	●	v ae au
Festuca spp	79	2	2-3-4	●	v ae au
Agropyrum spp	15	3	2-3-4-5	●	v ae au
Bromus spp	37	4	2-3-4-5	●	v ae au
Holcus lanatus	88	2	2-3-4-5	●	v ae au
Arrhenatherum avenaceum.	91	4	2-3-4-5	●	v ae au
Hordeum murinum	12	4	2-3-4-5	●	v ae au
Daucus Carota	8	3	1-2-3-4	●	v ae ae
Heracleum Spondyleum	54	4	1-2-3-4	●	ae au
[illegible]	2	5	3-4-5	●	v ae au

Aegopodium Podagraria	69	3	1-2-3-4	●	v ae au
Plantago major	53	2	1-2-3-4	●	v ae au
Plantago media	18	2	1-2-3-4	●	v ae au
Plantago lanceolata	27	3	2-3-4	●	Ø v ae au
Polygonum aviculare	31	3	2-3-4	●	Ø v ae au
Anthemis Cotula	29	4	1-2-3-4	●	Ø v ae au
Senebiera Coronopus	100	2	2-3-4-5	●	v ae au w
Trifolium repens	12	3	1-2-3-4-5	●	v ae
Papaver Rhoeas	31	2	1-2-3-4	●	v ae au
Ranunculus spp	12	3	1-2-3-4	●	ae au
Leontodon autumnalis	18	2	2-3-4-5	●	v ae au
Lamium album	62	2	1-2-3-4	●	v ae au
Rumex obtusifolius	14	2	3-4-5	●	v ae au
Nepeta hederacea	27	2	1-2-3-4	●	v ae au
Capsella-Bursa-pastoris	7	2	1-2-3-4-5	●	v ae au
Pteris aquilina					

TABLE X HEDGEROWS

IO EXAMPLES

DATE	20-5-32	22-5-32	29-5-32	8-8-32	8-8-32	12-8-32	30-8-32	9-9-32	12-8-32	30-8-32
	EX.I.	EX.II	EX.III	EX.IV	EX. V	EX.VI	EX.VII	EX.VIII	EX.IX	EX.X
SPECIES	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %	Frequency %
Crataegus Oxyacantha	82	92	92	82	100	100	81	100	78	100
Ulmus campestris		10		16						
Prunus spinosa			6				10			
Acer campestre			17	14			7		23	
Rubus fruticosus		11		29	16		62	9	80	18
Urtica dioica	63	76		92	32	110	64	57	18	
Galium Aparine			28	16						78
Anthriscus Sylvestris.	41	12	67							
Stellaria Holostea			7							
Lamium album	8	24	21					6		7
Achillea Millefolium		[illegible]	[illegible]		[illegible]	[illegible]	[illegible]		[illegible]	
Trifolium repens			5	8		42	24	9		

Trifolium repens				9			16	7	58	64
Heracleum Sphondyleum				11			41	9		
Peucedanum sativum									63	
Ranunculus spp		14								
Erysimum Cheiranthoides		12								
Leontodon autumnalis							63			
Centaurea nigra					8					
Scabiosa arvensis				2			6			
Lapsana communis					16		34			
Cirsium arvense		4		7			12		12	6
Hedera Helix	14					29	7	6		
Arrhenatherum avenaceum	21			98	62	18	70	96	23	84
Bromus sterilis	16	68	33					82		
Hordeum murinum	11	88	5							
Agropyrum repens	94	9	21	72	6	13				
Dactylis glomerata	12	44	18	16	47	29	52	17	100	100
Festuca ovina		9	27	16	100	100	96	41		
Holcus mollis				11	72	85	14	33		
Holcus lanatus		14		15				21		
Lolium perenne				8	71	37	7	11		
Poa pratensis	6			4	40	27	11			
Agrostis spp			5		57	6	39	92		

TABLE XI

AVERAGE OF 100 EXAMPLES

SPECIES	CONSTANCY	EXCLUSIVENESS	SOCIABILITY	VITALITY	PERIODICITY
Crataegus Oxyacantha	100	∅ 5	5	⊙	v ae au
Ulmus campestris	12	4	5	⊙	v ae au
Prunus Spinosa	17	∅ 5	2-3	⊙	v ae au
Acer campestre	13	∅ 5	2-3	⊙	v ae au
Rubus fruticosus	92	4	2-3	●	v ae au
Urtica dioica	100	3	2-3-4-5	●	v ae au
Galium Aparine	51	4	2-3-4	●	v ae au
Anthriscus Sylvestris	100	4	1-2-3-4-5	●	v ae
Stellaria Holostea	32	4	2-3-4	●	v ae au
Lamium album	29	3	2-3-4	●	v ae au
Achillea Millefolium	17	2	1-2-3	●	v ae au
Galium Mollugo	11	4	2-3-4	●	v ae au
Plantago spp	29	2	1-2-3	●	v ae au
Trifolium repens	100	2	2-3-4	●	v ae au w
Heracleum Sphondyleum	41	4	1-2-3-4	●	v ae au
Ranunculus spp	24	2	2-3-4	●	v ae au

Ranunculus spp	[illegible]				
Erysimum Cheiranthoides	7	2	1-2	●	v ae au
Leontodon autumnalis	9	2	1-2-3-4	●	v ae au
Centaurea nigra	21	2	1-2-3	●	ae au
Scabiosa arvensis	9	2	1-2	●	v ae au
Lapsana communis	7	3	1-2-3	●	v ae au
Cirsium arvense	91	2	1-2-3-4-5	⊙	v ae au
Hedera Helix	62	2	2-3-4-5	⊙	v ae au w
Arrhenatherum avenaceum.	100	4	2-3-4-5	●	v ae au
Bromus sterilis	64	3	2-3-4-5	●	v ae au
Hordeum murinum	9	3	2-3-4	●	v ae au
Agropyrum repens	82	3	2-3-4	⊙	v ae au
Dactylis glomerata	100	2	2-3-4	●	v ae au
Festuca ovina	100	2	2-3-4	●	v ae au
Holcus mollis	74	3	2-3-4-5	●	v ae au
Holcus lanatus	62	2	2-3-4	●	v ae au
Lolium perenne	100	2	2-3-4	●	v ae au w
Poa pratensis	92	2	2-3-4	●	v ae au w
Agrostis spp	61	2	2-3-4	●	v ae au

ø Artificially introduced, being utilised for this community and for no other purpose.

between fields.

In the case of the wayside quantitative data are given in the form of figures relating to the percentage frequency and percentage area covered (a measure of dominance) of the species. It is impossible to give figures relating to abundance of the species without producing very misleading data owing to the tillering habit and great density of certain species in proportion to others.

In the case of the hedgerow the peculiar configuration, arrangement and stratification of certain species makes even an estimation of percentage area occupied (dominance) a misleading and confusing statement. This is owing to the wide diversity of species from grasses to trees and climbing plants. The only quantitative data given here are those of percentage frequency of the species.

Qualitative data regarding species of the wayside and hedgerow are given in separate respective tables (Tables IX & XI). These include data regarding constancy, exclusiveness, sociability, vitality, periodicity.

Arrangement of the species and their zonation is illustrated by line transects (Transects 1-12) as well as by photographs.

In the case of each example in Tables VIII and X of wayside and hedgerow the dates of obtaining the data are given. Difference in dates of obtaining data explains why Anthriscus Sylvestris may occupy a more conspicuous position in some examples than in others.

In Table X the method of obtaining frequency data was to use a long lath instead of a quadrat. This instrument was laid against the bank and hedge, at intervals chosen at random, and in a position pointing vertically upwards. The incidence of the species was noted and from this the percentage frequency of each species was calculated.

It will be shown later that the stability or instability of the habitat, as the case may be, has a marked influence upon the type of vegetation. Stable habitats are dominated by perennial and gramineous species while unstable habitats are dominated by therophytic species, or by perennial species possessing runners which enable them to invade the habitat.

Examples III, IV, V, VII, VIII and IX, Table VIII, describe the vegetation of stable habitats of the wayside, while Examples I, II, VI and X of the same table are of unstable habitats.

In Table X, Examples I, II and IIIare those of very unstable habitats, while the remainder, Examples IV to VIII are of comparatively stable ones.

For convenience and facility, interpretation of the figures and symbols in Tables IX and XI, expressing qualitative characters, is repeated here.

Constancy. Number of cases in 100 examples in which species occurs.

Exclusiveness; Exclusive = almost confined to a given community. Preferential == preferring one community though growing more or less abundantly in others. Indifferent = preferring neither one community nor the other. Accidental = occurring accidentally.

Sociability: 1 = Single shoots. 2 = Shoots in small groups. 3 = Shoots in larger groups. 4 = Shoots in small colonies. 5 = Shoots in pure populations.

Vitality: ● Complete cycle regularly accomplished
⊗ - Cycle usually incomplete vigorous vegetative development.

θ Cycle incomplete restricted vegetative development.

⊙ Germinating accidentally not multiplying.

Periodicity: V = Vernal. ae = aestival. au = autumnal. w = winter.

Factors Affecting the Distribution and Arrangement of the Species

(1) The Marginal Region

The marginal region is that where the wayside joins the roadway, and may be described as the "gutter" region. The vegetation of this area varies somewhat, according to conditions. If there is a moist muddy condition where puddling occurs the vegetation is similar to that described as characteristic of gateways and cart tracks, (Fig. 45), Poa pratensis, Potentilla anserina, Plantago major, Matricaria suaveolens, Senebiera Coronopus and Polygonum aviculare are the most frequent species.

Poa pratensis, Matricaria suaveolens and Plantago major are usually locally dominant. In the case of these three species a distinct zonation may be observed. Matricaria suaveolens shows marked reaction to light as noted in the section dealing with gateways and cart tracks.

In cases where bare ground is found at the margin, owing to recent road making disturbance, there is always a marked abundance of therophytes. The most frequent species are in some cases Papaver Rhoeas, Anthemis Cotula, Hordeum murinum though these occur most commonly in the Eastern Counties of England. In other regions cruciferous species are most frequent.

When stable conditions exist in the marginal region the flora is similar to that of the grassland footpath. The species occur with the same abundance and frequency. Nearest the roadway is a zone of Poa pratensis followed by one of Lolium perenne and Trifolium repens. The phenomena are the same as those observed on the footpath, they are produced as the result of the same influences and therefore need no elaboration (Fig.46).

In the case of T. repens, however, there is a marked reaction to aspect at the wayside. The marginal region is frequently marked for miles by a zone of the white flowers of T. repens in the month of July. (Figs. 58, 59). A marked reaction to aspect is to be observed and is most obvious on roads running E - W. On the side with a southern aspect the flower heads are more abundant than on the opposite side.

It frequently happens that the marginal region is definitely and sharply demarcated from the road and is several inches higher than the "gutter". These cases occur in the absence of treading by human agency and the "footpath" type of vegetation is absent. The dominant species is most frequently Festuca ovina, but Dactylis glomerata is also locally dominant. (Fig. 47). In one instance (Thetford to Swaffham Road, Norfolk) the dominant species was Cerastium arvense, and here again marked reaction to aspect was noted. This reaction has also been noted on hedge banks in the case of Cerastium arvense.

(2) The Middle Region.

The above description denotes that part of the wayside lying between the marginal region and the inner boundary or hedgerow. In configuration it is usually slightly higher than the marginal region though frequently it may be at the same level, and is occasionally lower. The middle region may be intersected laterally by a footpath running parallel with the road, this frequently occurs but is not considered here being already dealt with in Section 3. A trench may also run parallel with the road, but is usually closer to the hedgerow than to the road. This trench is fed at intervals by tributary trenches running in from the road and serves as a soakaway.

Heaps of stone, gravel or sand usually line this middle region during certain parts of the year, generally spring and summer. These heaps vary greatly in size and distance apart and are a factor of great importance.

The deposition of sludge from the roadway and of rubbish from the hedgerow is a frequence occurrence, the wayside acting as a dump for many classes of material.

Frequent excavations occur in the form of trench making and cleaning. Road repairing results in the deposition of earth and other material, and along many main roads underground cable is laid in the middle region.

It will be seen that in the middle region there exist two types of habitat, i.e. the disturbed, and the stable or comparatively stable. The term stable is used for convenience, for it is rare to find a region which has been stable for any length of time. The whole of the wayside region must be regarded as made up of parts of a sere.

The vegetation of the middle region will be considered in two groups, i.e that of the comparatively stable habitat and that of the unstable.

(a) Stable Habitats.

Where disturbance is absent or not of recent date, the flora of the middle region exhibits a character which is remarkably constant for the waysides of Great Britain. The vegetation is in the main that of a meadow or pasture and contains the characteristic flora of these areas. This is explained by the fact that the area is always subjected to mowing at least once a year and in some districts to grazing. The former operation is a process in road cleaning, while the latter may be due to controlled grazing of cattle, or to sheep in hilly districts (Figs. 60, 61).

Where mowing or grazing by cattle are the chief factors the dominant species are Dactylis glomerata and Holcus lanatus with numerous others as sub-dominants. This is very typical of a neglected meadow or undergrazed pasture.

Where sheep are the chief factor, as in the Welsh hills or the Lake district, the whole wayside may be an Agrostis-festuca sward. A very similar vegetation is produced by rabbits when the wayside penetrates heaths or similar places where rabbits are abundant. There is, however, a slight difference, in that a greater proportion of Holcus spp appear to be present, possibly due to the absence of hoof action and to the close nibbling by rabbits.

Distinct zonation appears in the stable part of the middle region in the following arrangement. Where the middle region adjoins the outer, a zone of Bellis perennis may be found or of Plantago spp (other than Plantago major which is distinctly characteristic of the outer or "gutter" region.)

The above is superseded in autumn by a zone of Leontodon autumnalis. The above species are very charatteristic of this part of the stable middle region.

The following species Bellis perennis, Plantago spp and Leontodon autumnalis appear to be governed by the same factors. Owing to their prostrate foliage or rosette habit they are intolerant of shading and Leontodon at least exhibits marked reaction to light, being less abundant where the shadow of trees or of the hedgerow falls. * On the other hand they appear to be unable to tolerate severe treading. For these reasons they occupy a position where the light is able to penetrate, i.e. near the margin and yet sufficiently removed from the margin to escape heavy treading.

* This refers to Bellis perrenis and Leontodon autumnalis, and not to Plantago spp.

This phenomenon is often seen in the case of Bellis perennis at the margin of a footpath traversing a region which is undergrazed (Fig. 62) and resembles the wayside.

The dominance of Dactylis glomerata upon the stable middle region cannot be explained with perfect certainty. Its presence to such a degree is probably due to the fact that it does not tolerate very severe grazing or cutting and it here receives the optimum degree of such treatment. On the other hand it is a tall species which dominates all others in this region.

When Holcus lanatus occurs in any degree of abundance it always exhibits zonation (Figs. 63, 64). *The zone always corresponds with a very dry or very wet region, these conditions being produced by human agency, i.e. the cutting of a channel or formation of a high ridge. The most common situation for the zone of Holcus is on the brink of a channel, (Fig. 65), this region will be extremely dry owing to the effect of gravitation on the moisture content of the soil at this point. Holcus lanatus is found also as a zone in the bottom of some waterlogged channels where physiological drought may result. (Fig. 66). †The zonation of this species appears to be due to its xeromorphic adaptation to drought or physiological drought, occuring in habitats produced by human agency, and running parallel with the road.

(b) The Unstable Habitats

The nature of these regions has already been described as being due to excavation or the deposition of different types of material. Where there is a simple disturbance of the earth due to digging or to the baring of the turf or to a light surface deposition of earth,

+ For data see Section 10

† There is a good deal of controversy as to the true meaning of xerophytism. In this case it is taken as referring to a plant which tolerates drought conditions, the only xeromorphic character being the downy foliage.

the ground will be covered by a number of therophytes during the first season, these will in the second year give place to gramineous species.

There are two gramineous therophytes occurring on the above type of ground whose distribution is peculiar, i.e. Hordeum murinum and Bromus sterilis. The former species is chiefly confined to the Eastern side of England, but the distribution of the latter is general. Both species occur only upon bare earth or where a shallow deposit of sludge is present. Hordeum murinum occurs in scattered colonies, but Bromus sterilis* forms larger groups or consocies. Both species are conspicuous in appearance.

Hordeum murinum. This species occurs frequently in the following situations:-

At the ends of banks near gateways, dry parts of banks, sites of gravel heaps, at the base of posts or lamp posts.

In a journey of 61 miles (Norwich - King's Lynn - Stoke Ferry), Hordeum murinum was noted in 62 instances in all. Table XII shows the number of times out of the total of 62, in which it occurred on each of the 15 types of sites.

TABLE XII

Types of Habitats of Hordeum murinum	Number of sites on which species occurred.
Dry Banks.	16
θ End of Bank at Gateways.	23
* Bridges.	4
θ Lamp-posts	3
θ Telegraph-poles	2
θ Waysides. Site of Gravel heaps.	4
Heaps of Soil against Iron Railings	1
Disused Doorways in Wall.	2
Edge of Deep Channel	1
Base of Tree in Gravelled Area.	1
War Memorial.	1
θ Wayside. Newly raised for Road Camber.	1
Stone steps	1
Base of Wooden shed.	1
θ Wooden fence raised above Garden.	1
Total.	62

θ Illustrated in Figs. 67-73.

H. murinum usually most abundant directly over the tunnel.

The above sites all possess two characters in common,i.e. bare or deposited earth in conjunction with comparative dryness of the soil, both are induced by human agency. In Warming's system of "habitat forms" Hordeum murinum would be classed as a Chersophyte,i.e. a species inhabitating physically dry waste land.

In the above investigations care was taken to check the findings when making the same journey on subsequent occasions.

It is interesting to note the occurence on 23 occasions of the species at the extreme end of a bank. *It is quite obvious that this is the driest part of the bank as here the greatest surface area is exposed in proportion to volume of earth. It is a common practice to paste sludge cleaned from the gateway upon this part of the bank.

† It is clear from the above data that two factors influence the presence of Hordeum murinum,i.e. bare ground and dryness of the soil. Both factors are due to biotic agency, and it is notable that the species is more frequent in villages and suburbs than in open country as in the latter situation human activity is less intense.

<u>Bromus sterilis.</u> This is found on the site of deposited material or bare ground, chiefly the former. If an examination of any consocies of Bromus sterilis is carried out the above condition will be found at the base, (Fig. 74). The consocies may last several years due to re-seeding, but they gradually diminish in size. In the case of an old consocies the soil at the base may be obscured by the dead remains of last year's plants, but in

* For data, see section 10.

† In addition it is observed that by the mechanism of the awns, the seed may burrow its way into the soil. Like Poa annua, Hordeum murinum may have a very brief life, reaching maturity and seeding in a very short time when drought conditions prevail.

the majority of cases deposited material is to be found.

Agropyrum repens is a frequent occupant of the middle region of the wayside and is found to invade areas where earth has been deposited.

(c) Stone, Gravel and Sand Heaps.

Heaps of stone, gravel or sand possess a characteristic vegetation consisting in the main of species which are enabled to invade the heap by means of surface or underground runners. Agropyrum repens, Agrostis stolonifera and Potentilla anserina are frequent dominants or co-dominants of a heap. (Fig.75) Cirsium arvense is by far the most frequent dominant, though occasionally Urtica dioica may occupy this position. The distribution of the two latter species upon heaps is fully considered in special sections of this work, i.e. Sections 6, and 7. In these sections the peculiar influences exerted by the heap are fully discussed.

III. THE INNER, HEDGEROW OR BOUNDARY REGION.

The inner region of the wayside may also be described as the hedgerow or boundary region. It is characterised by a distinct type of vegetation and this associes is also found when a hedgerow forms a boundary between fields away from the wayside. It is advisable to consider the hedgerow and its vegetation as part of the wayside associes for the species of the former region merge into and invade the latter region.

Two types of habitat are again recognised i.e. the stable and the unstable. Whole hedge banks may be of the stable or unstable type, but in some cases a bank may possess intermittent areas of either type. The stable type is most frequent in the open country while the unstable is most frequent in the case of waysides occurring near towns, in suburbs and villages. The unstable condition is almost entirely due to the deposition of earth and sludge from roads or channels, to hedge cleanings or occasionally to the excavations of rodents. Figs.76,77, 78, give an illustration of the stable types and Figs.79, 80, 81 of the unstable (see also Transects 11 and 12).

Stable areas are characterised by perennial gramineous species, while unstable areas provide a habitat for certain therophytes, there being no pre-existing competition from gramineous species on the latter areas. Frequently,however, perennial species possessing runners will invade unstable areas when deposited material occurs.

Stable areas are occupied most frequently by such species as Arrhenatherum avenaceum, Festuca spp and Holcus mollis. Unstable areas are, on the other hand, usually characterised by Anthriscus sylvestris. *Smyrnium Olusatrum (near the seaboard), Heracleum sphondylium, Cirsium arvense, Urtica dioica, Lamium album, Aegopodium Podagraria, Agropyrum repens, Bromus sterilis Galium Aparine.

(a) Stable Habitats.

These are occupied mainly by four gramineous species, i.e Festuca ovina , Holcus mollis, Arrhenatherum avenaceum and Dactylis glomerata. All four species appear to be adapted to a dry habitat such as the bank provides. The two former species appear to possess the ability to exist upon poor shallow soil, Festuca ovina occurring sometimes upon bare rock. These two species possess a xeromorphic type of foliage. The two latter species appear to be adapted to a dry habitat in virtue of their deep root systems.

A distinct zonation of the species occurs upon hedge banks. Festuca ovina and Dactylis glomerata occupy

* The presence of Smyrnium near the seaboard, and its disappearance about a mile inland, is apparently due to the absence of frosts in the former region. There is a vigourous development of young foliage in December and January.

the sides of the hedge-bank, but do not grow in the actual hedgerow itself. Arrhenatherum avenaceum may sometimes grow in the hedgerow itself when the latter is thin, but usually occupies the outside of the hedge at the top of the bank. Holcus mollis will grow in the actual hedgerow in a peculiarly elongated form. (Fig 83)

Fig. 82 shows the zonation of Festuca ovina at the base of a hedge bank with a zone of Holcus mollis above, occupying the top of the bank. The factor governing this zonation is one of light, for both species are enabled to exist in equally dry situations, and in the absence of a hedge, Festuca ovina may occupy the top of the bank in the place of Holcus mollis.

Festuca ovina is too low in habit to compete for light and cannot penetrate the hedgerow. On the other hand Holcus mollis is peculiarly adapted to overcome the shading influence of the hedge. In this latter situation the runners penetrate the loose debris at the base of the hedgerow and send up long stems with very lengthy internodes. Shoots develope at the nodes and will, in the presence of moisture, develope a root system also. The whole plant takes on the appearance of a climber and functions as one. Fig 83 gives an illustration of this adaption. The same phenomenon is sometimes observed in the case of Agrostis spp. though not so commonly as with Holcus mollis. Occasionally both species may grow together.

<u>Distribution of Arrhenatherum avenaceum.</u> The constancy of this species on hedge banks, and at the inner region of the wayside renders the factors governing its

distribution worthy of consideration. A perusal of the line transects in this section illustrates the preference exhibted by the species for ungrazed and protected positions.

The above phenomenon is to be observed in all parts of the country, the species appearing to be adapted to many types of soils.

The tallness of the species enables it to compete with the hedge for light, but it is also found in other protected positions where light competition does not exist. Figs. 84, 85 shew typical situations of Arrhenatherum avenaceum

Soil moisture does not appear to be a factor of any importance. A study of the distribution of this species on Boughton Fen (Norfolk) shewed it to exist on a soil of all degrees of moisture from a waterlogged condition to a very dry one. Fig. 86 shows consocies of Arrhenatherum avenaceum in waterlogged hollows in Boughton Fen. There is a zone dominated by Dactylis glomerata in the foreground, this is the wayside. Fig. 87 shews the species dominating an inaccesible and ungrazed background, here the soil ranges from the waterlogged to the dry condition, through all degrees of moisture.

It appears obvious that the factor controlling the presence or absence of the species is the absence or presence of the biotic factor in the form of treading or grazing. It is well known to agriculturists that this species is not tolerant of grazing or disturbance (13). All the sites both in the line transects in this section and in the illustrations, in which Arrhenathenum avenaceum occurs, are sites protected from grazing or treading.

Fig 88 shews the species growing on the side of the hedge nearest the road, but absent on the field side where grazing by sheep occurs. Fig. 89 shews the species growing on both sides of the hedge, the road being on one side, an arable field on the other.

There appears no doubt that the inhibiting factor is in this case a biotic one, the species being intolerant of grazing or treading and only existing in sites protected or removed from these influences, (Fig. 90). In life form the species is a chamaephyte.

(b) The Unstable Habitat

As in the case of the other regions of the wayside, the hedge bank possesses unstable areas chiefly owing to the deposition of earth, sludge and other refuse. *These areas are characterised by therophytes or by perennials possessed of runners.

The dominant species most characteristic of these regions are Anthriscus sylvestris (in the vernal period) Smyrnium Olusatrum (near the seaboard S and S.E. England). Cirsium arvense, Agropyrum repens, Urtica dioica, Lamium album and Aegopodium Podagraria.

Distribution of Anthriscus sylvestris

This species occurs as a dominant of the hedge bank during the month of May. It originates upon areas where earth and sludge have been deposited and may also invade these areas of the wayside or occupy channels cut at the wayside. Strong colonies grow on these bare areas, but diminish in size if fresh material

* Anthriscus sylvestris, Smyrnium Olusatrum and Heracleum Sphondylium are exceptions. The former is a perennial and the two latter biennials, none being possessed of runners

Dense colonies of these species may remove grass competition from their habitat by their smothering effect.

is not deposited the following year, and grasses invade the area.

The species shows a remarkable reaction to aspect being more abundant upon a side of the bank with a southern aspect than of that with a northern. When a bank runs from North to South the species may be equally abundant on either side. Figs. 91, 92, 93 illustrate these points.

Anthriscus sylvestris is extremely intolerant of grazing by sheep which are partial to the plant. Fig 94 shows the species on either side of a hedge running North to South where an arable field occurs on one side and a road on the other. On the opposite side of the road a pasture occurs where sheep are constantly grazing, the species is absent on the pasture side of the field but not on the road side,(Fig. 95). Further along this field there is an area adjoining the hedge, on the pasture side, which is protected by sheep netting, here the species is seen growing (Fig 96).

It may be noted that Figs. 94, 95, 96, in the above paragraphs are taken on the same sites, though earlier in the year, as Figs. 88, 89, dealing with the influence of sheep upon Arrhenathenum avenaceum. A comparison of Figs 94, 95, 96 with Figs 88, 89, gives an illustration of the sequence of species from the vernal to the aestival period.

*Heracleum Sphondylium usually succeeds Anthriscus sylvestris and while the former species occurs most abundantly upon bare ground it is more tolerant of grass competition than Anthriscus sylvestris. Fig 97 shews a typical zone of this species.

* This does not imply succession in the ecological sense. Anthriscus sylvestris dominates the vernal aspect and Heracleum Sphondylium the aestival and autumnal aspect.

Cirsium arvense is a frequent occupant of bare ground on the hedge bank, but a special section of this work is devoted to its distribution and any discussion here would be superfluous.

Agropyrum repens invades bare ground by means of its underground runners, and also may occupy an area covered by any loose material. This species appears to require a loose medium for the proliferation of its runners, it is not frequent upon heavy or consolidated soils.

The Distribution of Urtica dioica, Lamium album and Aegopodium Podagraria

The distribution of these species is treated as one problem, as they are all of practically the same life form and dependent upon the same factor for their distribution.

Aegopodium Podagraria presents several unusual features with regard to its distribution. It is most frequent on hedge banks outside or adjoining a garden.
The following data were obtained during three journeys:-

(1) Norwich to King's Lynn via Bawdeswell, 39 miles
(2) Wisbech to King's Lynn, via Outwell, 22 miles
(3) King's Lynn - Watton - Shipdham - N.Pickenham - Swaffham, 40 miles.

In a total distance of 101 miles, 63 colonies of Aegopodium Podagraria were noted. The figures set out in Table XIII give the situations of the colonies.

Table XIII

Types of Habitats of Aegopodium Podagraria	Number of sites on which species occurred.
Ø Bank outside Garden	42
Bank opposite Garden	11
Bank outside Paddock	1
Fence on Bridge	1
Road Corner	1
Wayside	3
Hedgerow	4
Total	63

Ø Illustrated in Fig. 98

It will be seen from the above table that out of a total of 63 sites on which the species occurred, on 42 occasions the plants were growing immediately outside a garden hedge, and on 11 occasions on a bank opposite a garden.

On all occasions upon which the species has been observed it has been found in conjunction with some loose surface material, such as garden refuse, which provides a cover for the runners. †It will be seen later that this factor is also the main influence in the case of Urtica dioica and Lamium album.

The loose rubbish may provide a medium for the runners to protect them from the influence of light or desiccation. *In the case of this species the runners are found on or immediately below the soil surface. The influence of this surface cover and the dependence of the above three species, of the same type of life form, upon its presence, is fully discussed in Section 6 of this work.

It is obvious that surface cover occurs in many other situations than the proximity of gardens and it is difficult to explain the affinity of the species for this position. The only rational explanation appears to be the fact that the species was much cultivated in gardens as a medicinal herb (14). Owing to its dependence upon bare ground or surface cover it has not spread far in competition with grasses. The species is a serious weed in market gardens in the fens. The seed is not wind borne, or easily distributed.

Urtica dioica is almost a constant species of the hedgerow, and frequently advances therefrom to the wayside As this species is a characteristic one of many areas of semi-natural vegetation, it receives separate treatment in Section 6. This fuller exposition is also necessary

* Fig. 99.A. Illustrates the life form of this species.

† Aegopodium Podagraria frequently forms a synusid with Urtica dioica and Lamium album. Fig. 99. B.

owing to the writer's contention that the distribution of the species is governed by the presence of surface cover in some form or other and further owing to the refutation of the orthodox belief that Urtica dioica is a nitrophilous plant.

*The above remarks also apply to Lamium album which usually occurs in association with colonies of Urtica dioica.

For the purposes of this section it must be assumed that both Urtica dioica and Lamium album owe their presence in the hedgerow to the surface cover provided by debris and further that their advance from the hedgerow is owing to the deposition of surface cover of some type in the proximity of the hedge.

The Hedge.

The shrubs and trees which form the hedge proper have been enumerated already, but Figs. 101-104 and Figs. 49-57, give illustrations of the appearance of these species in the actual position.

The type and configuration of the hedge depends mainly on the taste and skill of the hedger. The chief species such as Crataegus Oxyacantha are usually planted in the first place as cuttings or seedlings, but other species may be introduced vegetatively or from seed dropped by birds. Ulmus campestris may form a hedge by means of "suckers" from large trees, if carefully trained by the hedger. (Fig. 100). This species if untrained may send suckers out into the wayside and ultimately form a thicket there.

In arable districts a thin wall shaped hedge may suffice as a simple boundary between fields, Figs. 101, 102, but in grazing districts a thicker and more

* Mercurialis perennis has a similar life-form, and is regarded as a shade species. It frequently occurs in exposed situations, but is always found in association with loose litter, usually dead leaves. Under trees it usually coincides exactly with the zone covered by dead leaves.

impenetrable type is necessary, (Fig. 103). Hedges may also be used as wind breaks and as such will also cause considerable overshadowing of surrounding vegetation, Fig.104.

In the case of an arable land hedge the height is regulated by chopping off as required and the width regulated by trimming or "brushing" with a bill hook.

In forming a hedge as a barrier against stock a procedure known as "pleaching" or "laying" is carried out. The trunks of shrubs and trees are cut slantwise and downwards at the bottom, but not cut completely through. They are then bent over. The piece left unsevered serves as a channel for sap from the roots to the bent over trunk. The stump is well trimmed. Figs. 105.106, illustrate this process carried out by a skilled hedger. Fig 107, shews a piece of faulty workmanship.

Where the work is carried out by a bad craftsman using blunt tools and where jagged edges and untrimmed stumps are left, fungus disease enters and causes, ultimately, gaps in the hedge.

Climbing Species.

The hedge when left untrimmed and unweeded always suffers from the competition of climbing species which grow from the base of the hedgerow, derive support from the hedge and eventually smother it. The chief species are Rubus fruticosus, Convolvulus sepium Galium Aparine and occasionally Humulus Lupulus. This smothering effect is illustrated in Figs.108, 109, 110. These illustrations shew the effect of Convolvulus sepium Rubus fruticosus and Humulus Lupulus respectively.

Conclusions.

It is seen that while the vegetation of wayside and hedgerow is typically semi-natural, it is also influenced by the natural type of vegetation which it intersects.

In spite of external influences the biotic factor, in its various manifestations, produces a definite wayside and hedgerow type of vegetation arranged in the main into zones.

Two sub-types may be recognised, i.e. the type characterising a comparatively stable habitat and that of an unstable habitat.

The chief influences which produce the flora of wayside and hedgerow and its arrangement are the influence of treading, grazing and mowing, and conversely protection from these influences as in the case of Arrhenathenum avenaceum.

Admission or restriction of light produces zones of certain species as does artificially induced drought.

The deposition of different types of material, stones, gravel, sand, sludge and organic matter gives rise to colonies of certain characteristic species.

Fig.43. Pteris aquilina invading wayside from a colony of Pteris aquilina on adjoining heath (Grimston , Norfolk).

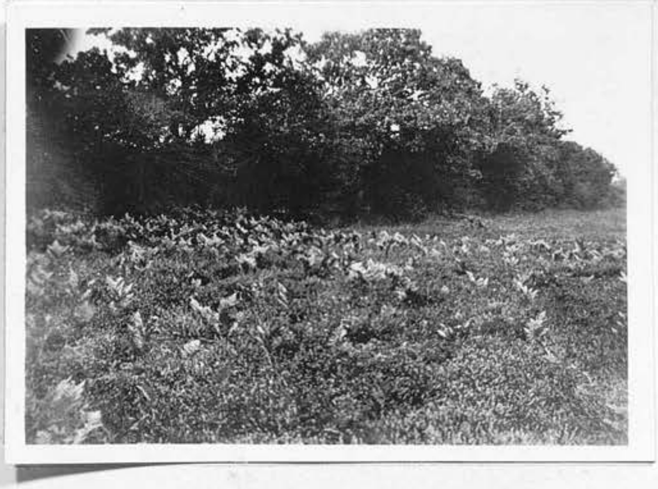


Fig.44. Showing colony responsible for invasion shown above (Fig.43) (Grimston, Norfolk.)

Extended view

Close view shewing associes of Plantago major. Matricaria suaveolens and Polygonum aviculare

Fig.45. Marginal region of wayside. Frequently disturbed area. (Gaywood, Norfolk).

Fig.46. Marginal and middle regions of wayside utilised as a footpath. (Wells-next-sea. Norfolk).

Fig.47. Marginal region of wayside, undisturbed and untrodden. (Nr. Fakenham, Nofolk.)

Fig.48. Zone of Leontodon autumnalis between marginal and middle region of wayside. (Boughton, Norfolk).

Fig.49. Elm Hedge. (Ulmus campestris). (Middleton, Norfolk).

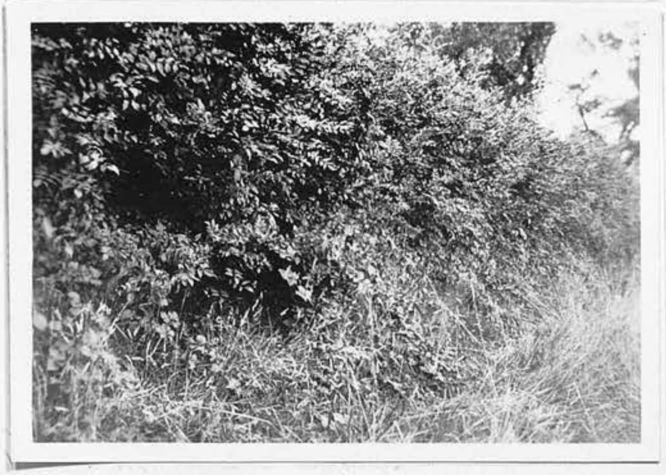


Fig.50. Ash hedge (Fraxinus elatior).

Fig.51. Beech hedge (Fagus sylvatica) (Hawkshead, Westmoreland)

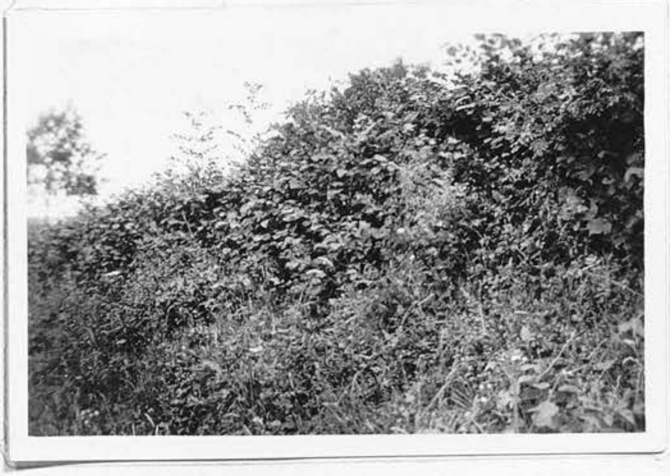


Fig.52. Hazel hedge (Corylus Avellana).(Newtown, Montgomeryshire).

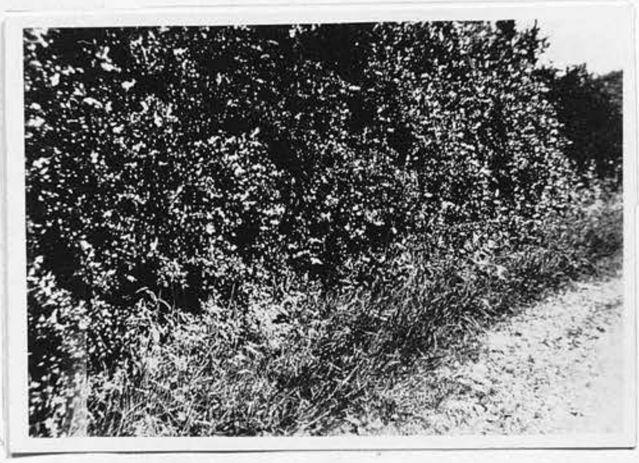


Fig.53. Holly hedge (Ilex Aquifolium) (Newlands,Cumberland)

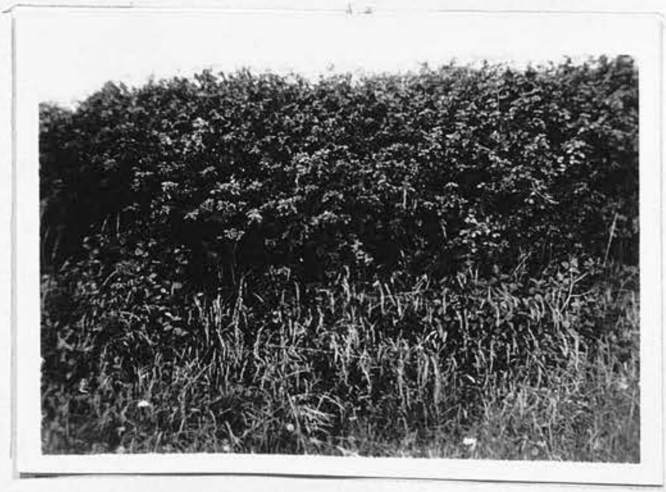


Fig.54. Maple hedge (Acer campestre) (E.Rudham,Norfolk).

Fig.55. Dogwood hedge.(Cornus sanguinea) (Stow Bardolph, Norfolk).

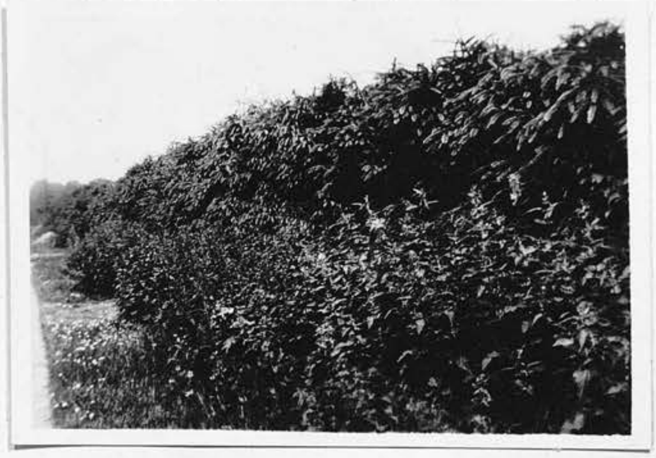


Fig.56. Coniferous hedge (Picea alba).(Cockley Cley,Norfolk)

Fig.57. Coniferuous hedge (Pinus sylvestris) (Cockley Cley,Norfolk).

Fig.58. Growth of Trifolium repens at margin of wayside. Southern aspect. (Nr.Cambridge).

Fig.59. Extended view of Fig 58. above (Nr.Cambridge).

Fig.60. Frequently mown wayside.(Boughton,Norfolk.)

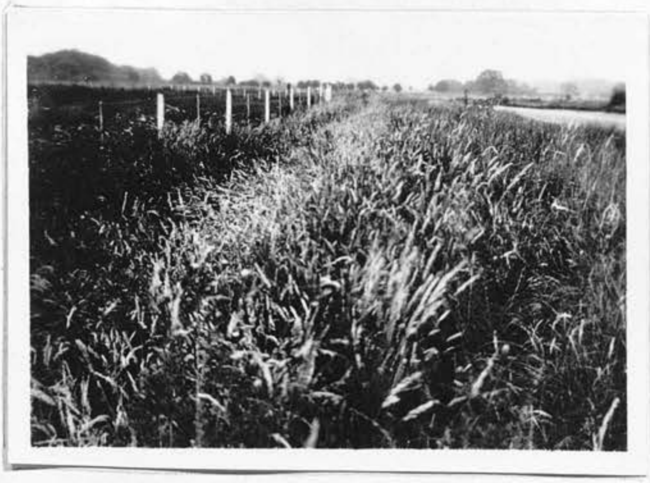


Fig.64. Zonation of Holcus lanatus at brink of ditch.
(Babingley, Norfolk).

Fig.65. Close view of Holcus lanatus zone, illustrated in fig.63. Note absence of the species on opposite side of channel owing to moisture due to gravitation. from bank.

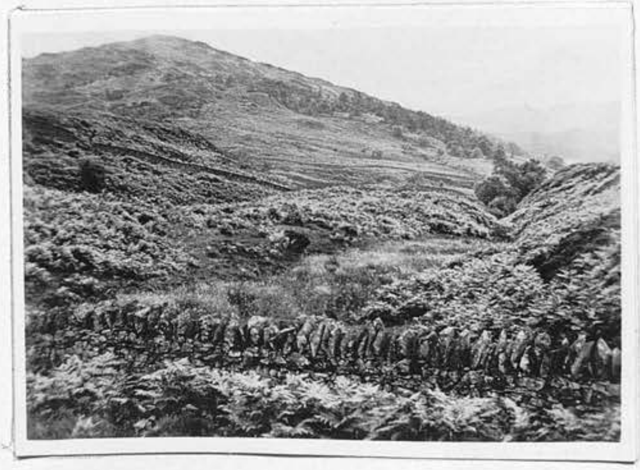


Fig.66. Colony of Holcus lanatus in waterlogged hollow.
(Nr. Tarn Howes Lake District).

Fig.70. Hordeum murinum at base of telegraph pole.
(Gaywood, Norfolk).

Fig.71. Hordeum murinum on site of former gravel heap.
(Dersingham, Norfolk).

Fig.72. Hordeum murinum at wayside where ground was recently raised to allow for camber at bend of road.
(Nr. Fincham, Norfolk.)

Fig.73. Hordeum murinum at base of fence on pavement side. Garden beyond fence at lower level.(Gaywood Norfolk).

Fig.74. Colony of Bromus sterilis dominating heap of sludge at wayside. (Oswestry Salop).

Fig.75. Agropyrum repens and Potentilla anserina colonising sand-heap (Salter's Lode,Norfolk)

Fig.76. Stable banks dominated by Dactylis glomerata, Arrhenatherum avenaceum, Festuca spp, Agrostis spp, Rubus fruticosus etc. (Flitcham, Norfolk).

Fig.77. Wayside and bank dominated by Dactylis glomerata, Arrhenatherum avenaceum, Festuca spp, etc. Stable side of road of Fig.77 (Nr. Syderstone, Norfolk.)

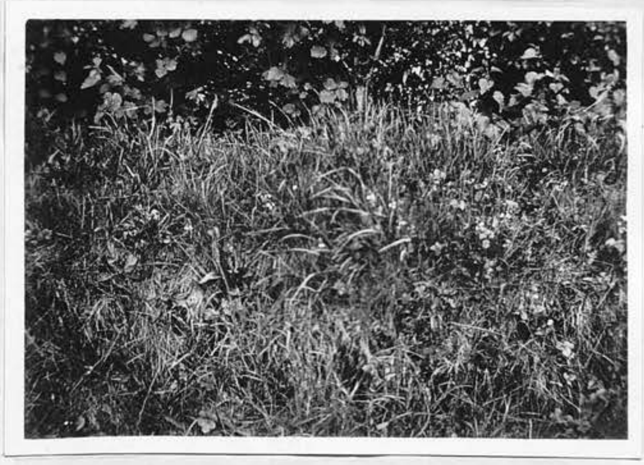


Fig.78. Stable bank --dominated by Festuca ovina spp. Agrostis stolonifera, Dactylis glomerata, Rubus fruticosus with Lamium album as a sub-dominant. (Fakenham, Norfolk).

Fig.79. Unstable bank dominated by Agropyrum repens,(Gaywood, Norfolk).

Fig.80. Unstable wayside and bank dominated by Anthriscus sylvestris, Urtica dioica etc.(Nr.Syderstone,Norfolk.)

Fig.81. Unstable bank dominated by Lamium album,Urtica dioica Anthriscus sylvestris, Cirsium arvense and Agropyrum repens (Gaywood,Norfolk).

Fig. 82. Stable bank showing zonation of species. (a) Light zone of Holcus mollis at top of bank under shade of hedge. (b) Dark zone of Festuca ovina spp at lower part of bank. (c) Bellis perennis at foot of bank and margin of footpath. (d) Footpath. (e) Pasture. (Norfolk Agricultural Stn. Sprowston).

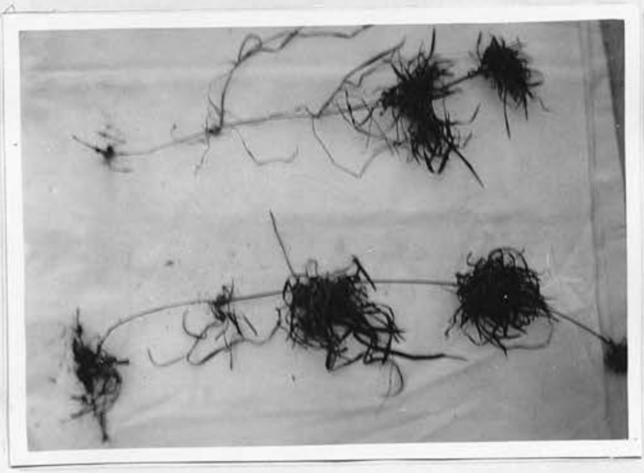


Fig. 83. Holcus mollis from hedgerow. Note shoots at nodes and aetiolated internodes.

(Illustration shown horizontally)

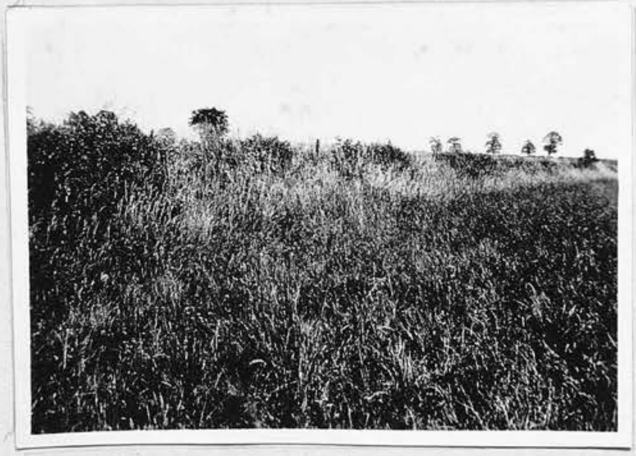


Fig. 84. Typical zone of Arrhenatherum avenaceum on stable hedge bank. Foreground which is frequently mown, dominated by Dactylis glomerata.

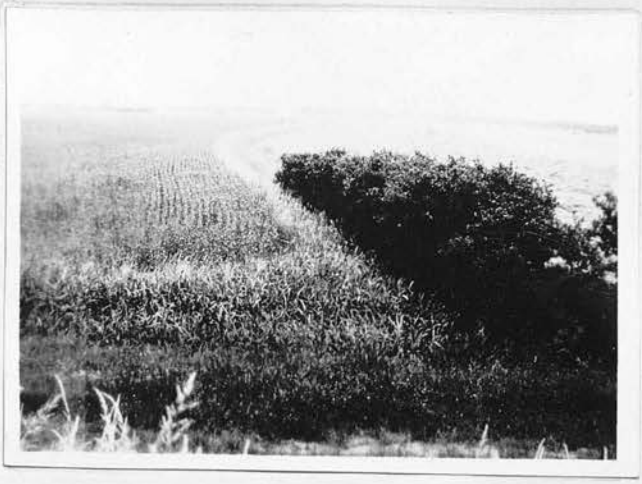


Fig.85. Zone of Arrhenatherum avenaceum along margin of ditch (W.Walton,Wisbech).

Fig.86. Consociation of Arrhenatherum avenaceum,in waterlogged ungrazed reed-swamp.(Wayside association in foreground). (Boughton Fen,Norfolk).

Fig.87. Consociation of Arrhenatherum avenaceum on ungrazed and unmown ground beyond reed swamp. The ground populated by Arrhenatherum varies with level from a wet to a dry state.(Boughton Fen,Norfolk).

Fig.88. Arrenatherum avenaceum on road side of hedge on ungrazed and unmown region. Note absence of the species on pasture side of hedge. Note also presence of Heracleum Sphondylium on road side of hedge. (Runcton, Norfolk).

Fig.89. Arrhenatherum avenaceum present on both sides of hedge. The field is under arable cultivation. Heracleum Sphondylium also present.(Opposite side of road to fig.88.)

Fig.90. Showing absence of Arrhenatherum avenaceum, where protection from grazing has been broken down. (Terrington Marsh, Norfolk).

N.

S.

Fig.91.Showing presence of Anthriscus sylvestris on bank with southern aspect. Absent on side with northern aspect (Fakenham Norfolk).

S.

N.

Fig.92. Showing presence of Anthriscus on side of bank with southern aspect. Absent on side with Northern aspect.(Gayton,Norfolk).

S.

E.

W.

N

Fig.93.Showing presence of Anthriscus on both sides of hedge running North to South and consequently receiving equal illumination on both sides. (Runcton,Norfolk).

Fig.94. Showing Anthriscus sylvestris on both sides of hedge (running North to South). Arable field on East side roadway on West. (Runcton, Norfolk).

Fig.95. Showing absence of Anthriscus on pasture side of hedge (running South to North on opposite side of road to Fig.94 (cf Figs.88,89,90), pasture grazed by sheep and cattle.

Fig.96. Showing portion of hedge in Fig.95 above, protected by sheep netting and showing Anthriscus growing i the enclosure, where sheep are excluded.

Fig.97. Typical zone of Heracleum Sphondylium. Note also Arrhenatherum avenaceum (Tattersett, Norfolk).

Fig.98. Colony of Aegopodium Podagraria on bank outside garden (Wretton, Norfolk).

A. B.

Fig.99. A, Life Form of Aegopodium Podagraria.

B. Synusia of Aegopodium Podagraria, Lamium album and Urtica dioica.

Fig.100. Hedge formed from suckers from elm trees (Ulmus campestris) (Clenchwarton,Norfolk).

Fig.101. Typical arable land hedge. Hawthorn . (Crataegus Oxyacantha). Clenchwarton,Norfolk).

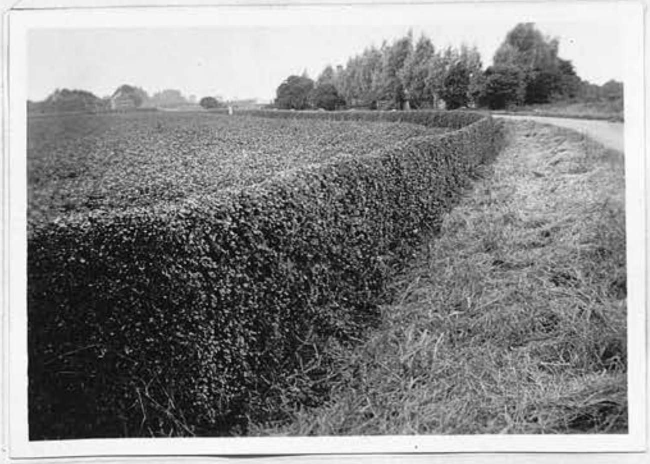


Fig.102. Hawthorn hedge in intensively cultivated district (Upwell,Isle of Ely).

Fig.103. Hedge with broad base tapering to a sharp apex. Typical hedge of grassland district where a barrier against livestock is necessary. (Runcton,Norfolk).

Fig.104. Hedge used as wind-break.Typical of flat exposed country.(Gayton,Norfolk).

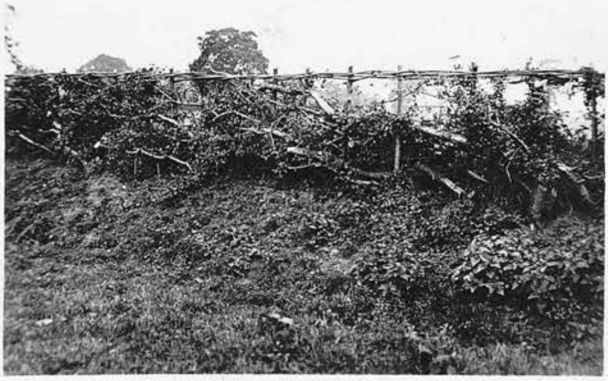


Fig.105. The "Pleached" or "Laid" hedge.(Norfolk Agricultural Stn.Sprowston.)

Fig.106. The method of pleaching by cutting, and bending or "laying" the trunks of the trees. Note trimmed stumps. (Norfolk Agricultural Stn. Sprowston)

Fig.107. A badly "pleached" hedge. (Hawkshead, Lancashire)

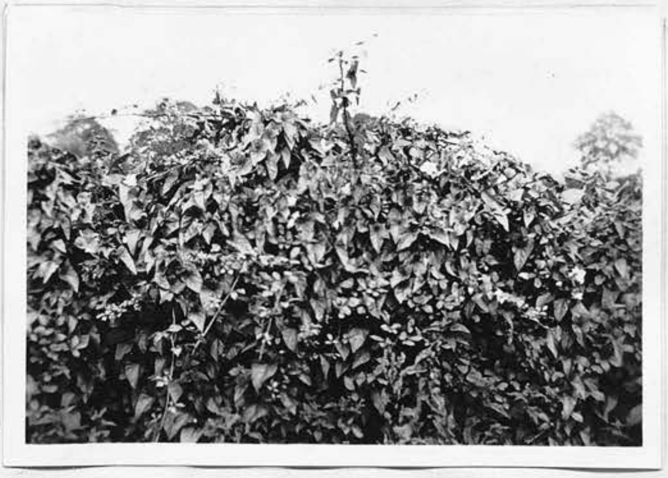


Fig.108. Hedge smothered by Convolvulus sepium. (Stow Bardolph, Norfolk.)

TRANSECTS
1 - 12.

(SECT. 5)

Symbols Denoting Species	Transects 1-12

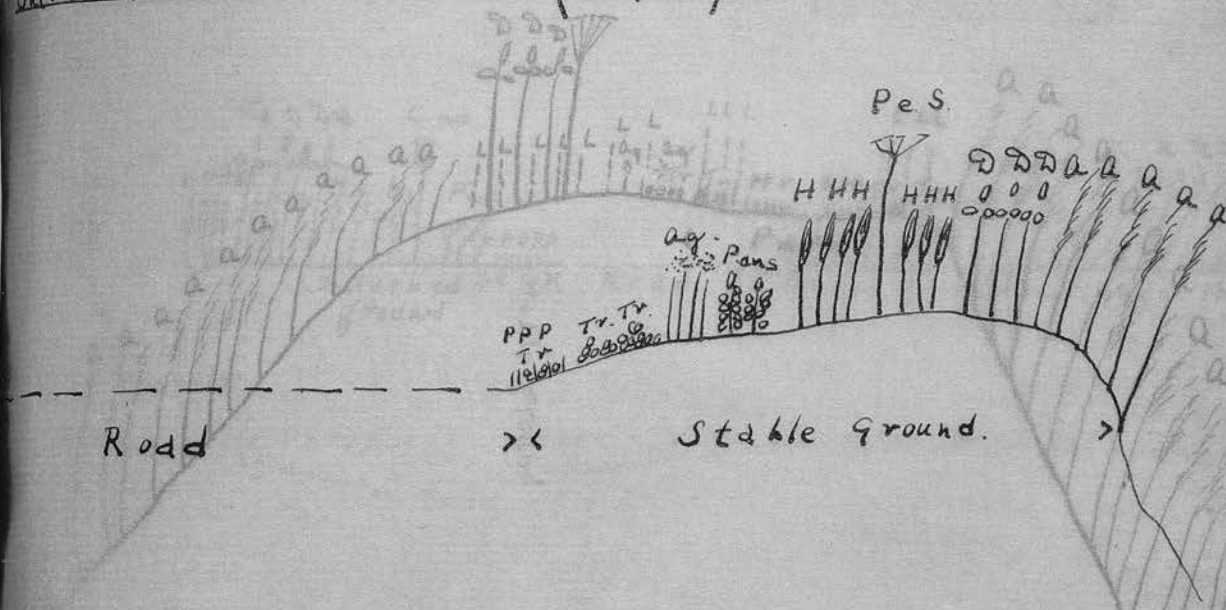
A	Arrhenatherum avenaceum
Ag	Agrostis stolonifera
A.M.	Achillea Millefolium
A.r.	Agropyrum repens
A.s.	Anthriscus sylvestris
B.p.	Bellis perennis
C.ar.	Cirsium arvense
C.Ox	Crataegus Oxyacantha
D.	Dactylis glomerata
F.	Festuca ovina
Fe	Festuca elatior
H.S.	Heracleum Sphondylium
H.	Holcus Lanatus
H.m.	Holcus mollis
H.mu.	Hordeum murinum
L.	Lolium perenne
L.al	Lamium album
L.au	Leontodon autumnalis
M.s.	Matricaria suaveolens
N.p.	Nepeta hederacea
P.	Poa pratensis
P.ans	Potentilla anserina
P.av	Polygonum aviculare
P.m.	Plantago major
P.R	Papaver Rhoeas
P.s	Peucedanum sativum
R.	Ranunculus spp
R.o.	Rumex obtusifolius
S.l.	Scirpus lacustris
T.r.	Trifolium repens
U.	Urtica dioica.

N.B. Symbols do not denote relative abundance of the species but indicate distribution.

Trans 1

Outwell Fen. Middle Level Rd (Norfolk)

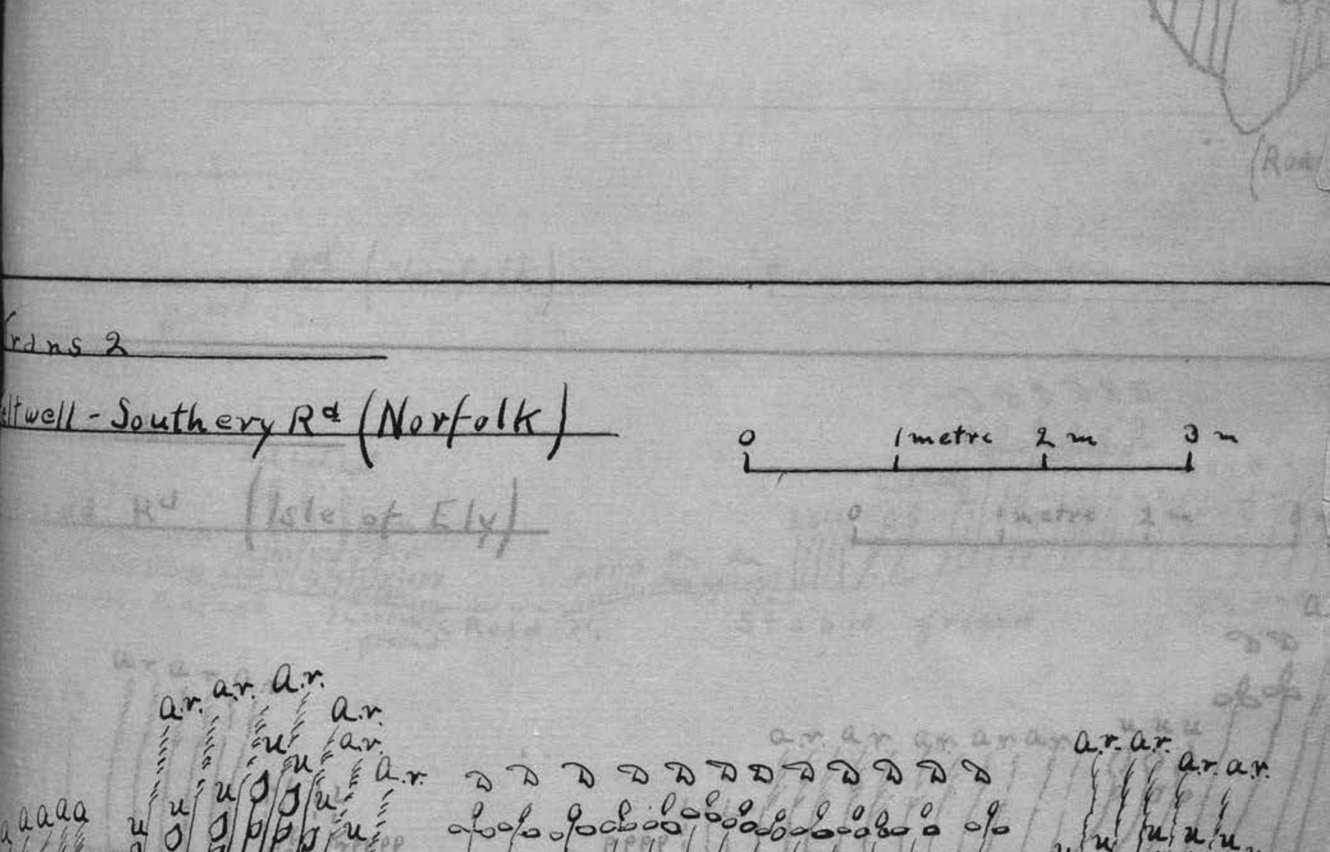
0 1 metre 2 m 3 m



Trans 2

Outwell - Southery Rd (Norfolk)

0 1 metre 2 m 3 m



Transects 1-12

Symbols Denoting Species

A Arrhenatherum avenaceum

Ag Agrostis stolonifera

A.M. Achillea Millefolium

A.r. Agropyrum repens

A.s. Anthriscus sylvestris

B.p. Bellis perennis

C.ar. Cirsium arvense

C.Ox Crataegus Oxyacantha

D. Dactylis glomerata

F. Festuca ovina

Fe Festuca elatior

H.S. Heracleum Sphondylium

H. Holcus Lanatus

H.m. Holcus mollis

H.mu. Hordeum murinum

L. Lolium perenne

L.al Lamium album

L.au Leontodon autumnalis

M.s. Matricaria suaveolens

N.p. Nepeta hederacea

P. Poa pratensis

P.ans Potentilla anserina

P.av Polygonum aviculare

P.m. Plantago major

P.r. Papaver Rhoeas

P.s Peucedanum sativum

R. Ranunculus spp.

R.o. Rumex obtusifolius

S.l. Scirpus lacustris

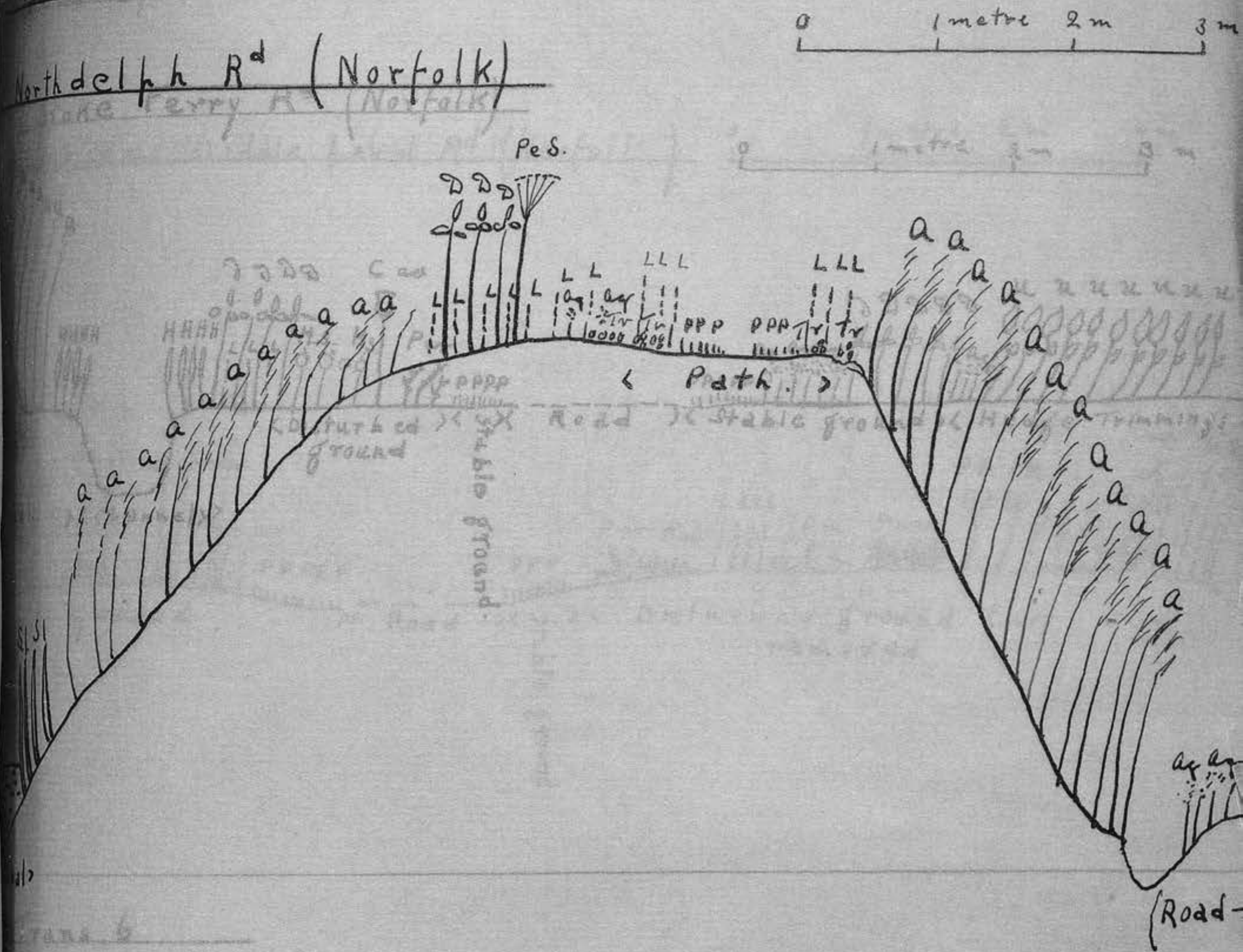
T.r. Trifolium repens

U. Urtica dioica.

N.B. Symbols do not denote relative abundance of the species but indicate distribution.

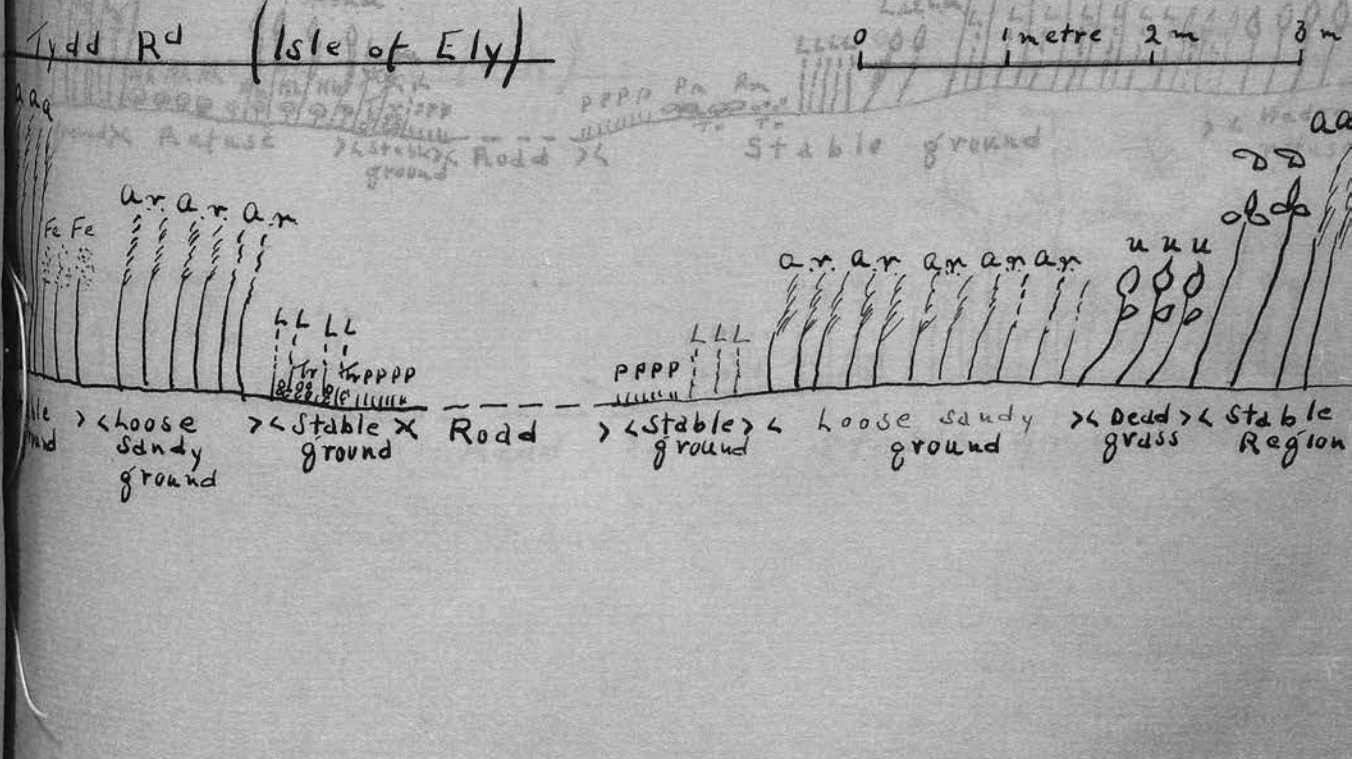
Trans 3

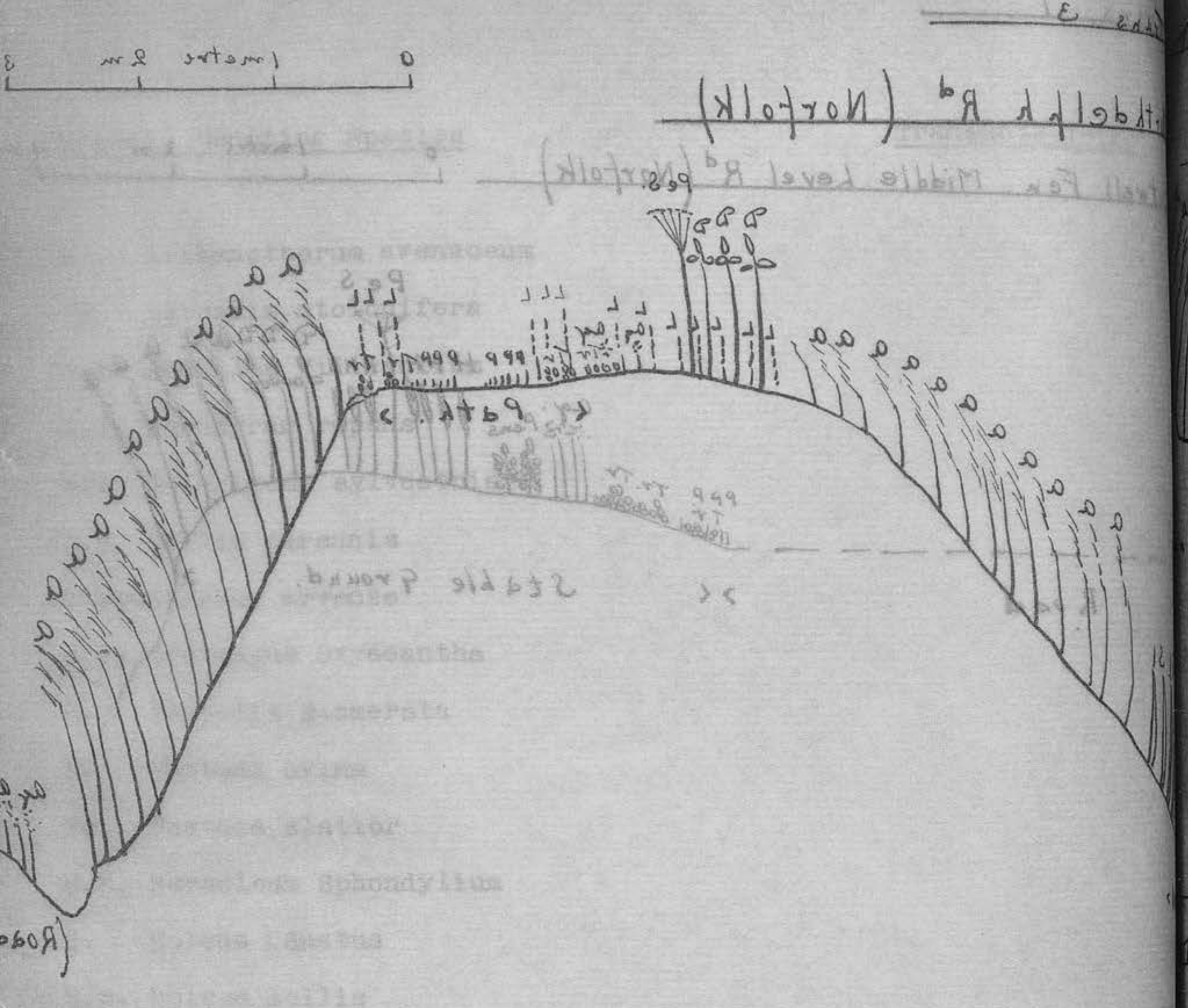
Northdelph R^d (Norfolk)

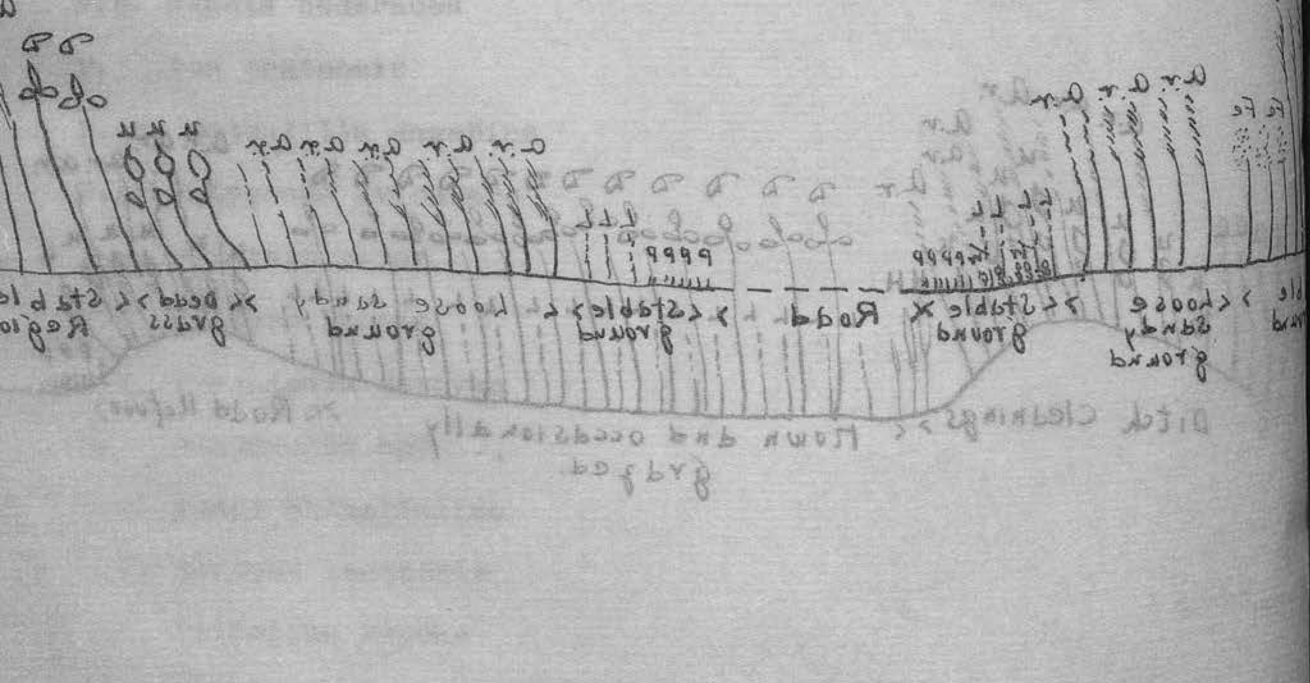


Trans 4

Tydd R^d (Isle of Ely)

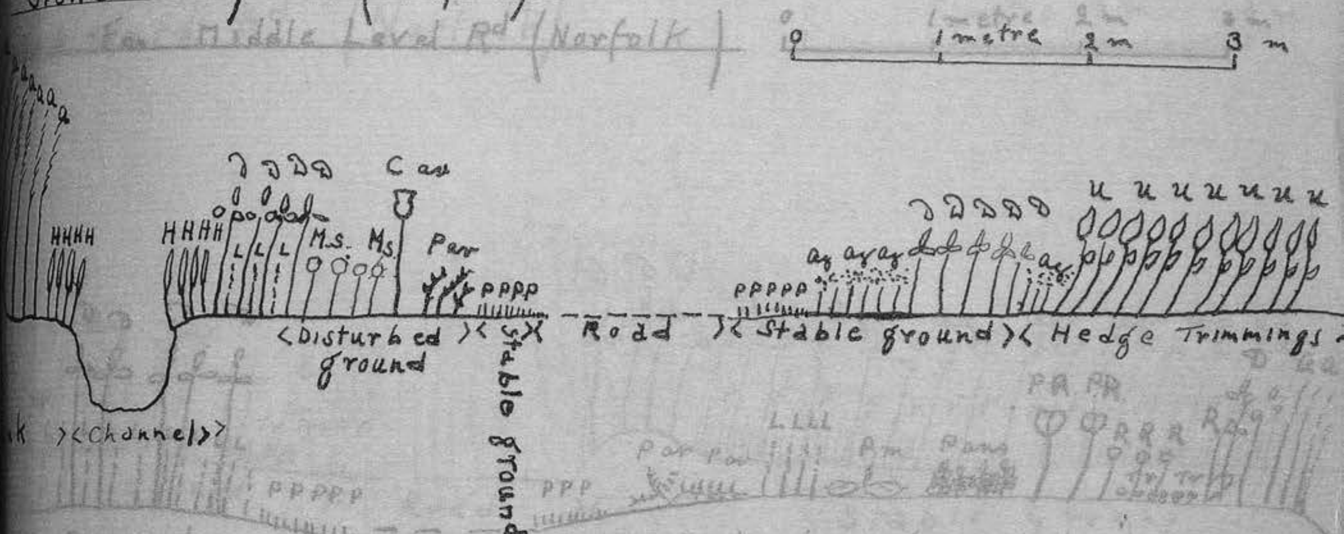



(Norfolk)
Middle Level Rd (Norfolk)
Path
Stable ground
Road
1 metre 2 m 3


(Norfolk)
Rd (Isle of Ely)
1 metre 2 m 3
Road
Stable
Loose sandy ground
Stable ground
Ditch cleanings, mown and occasionally dug.
Road Refuse

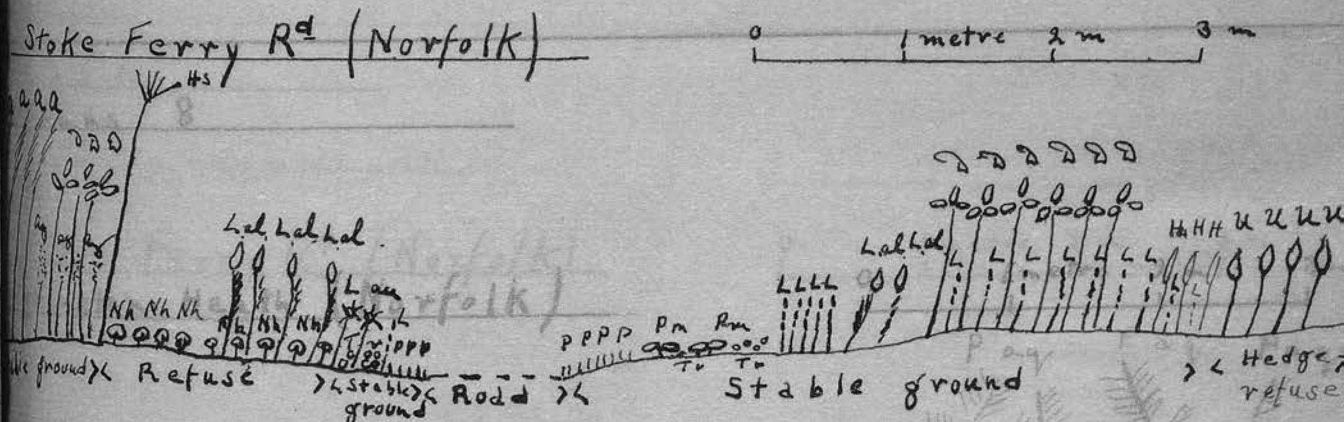
Trans 5

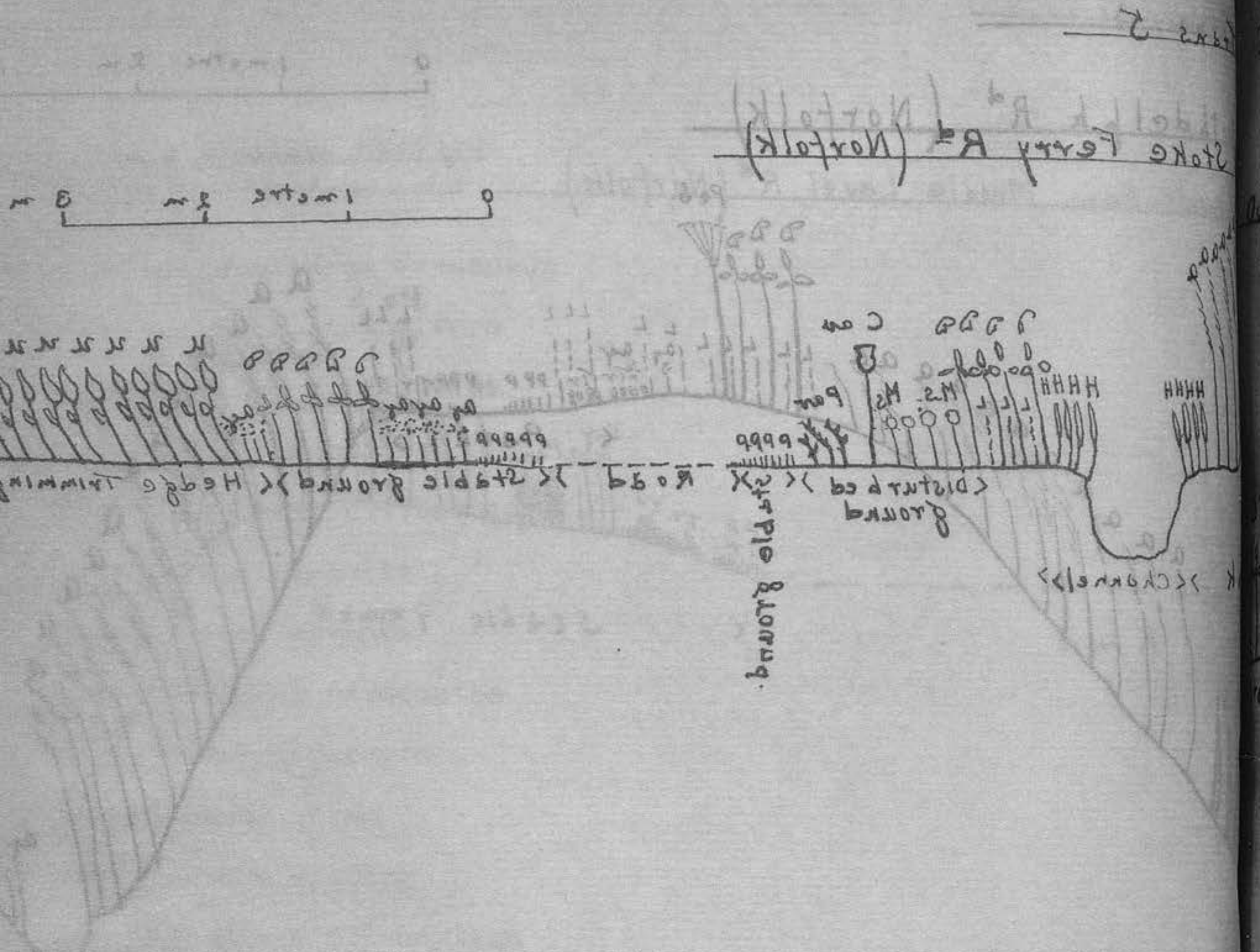
Stoke Ferry Rd (Norfolk)



Trans 6

Stoke Ferry Rd (Norfolk)

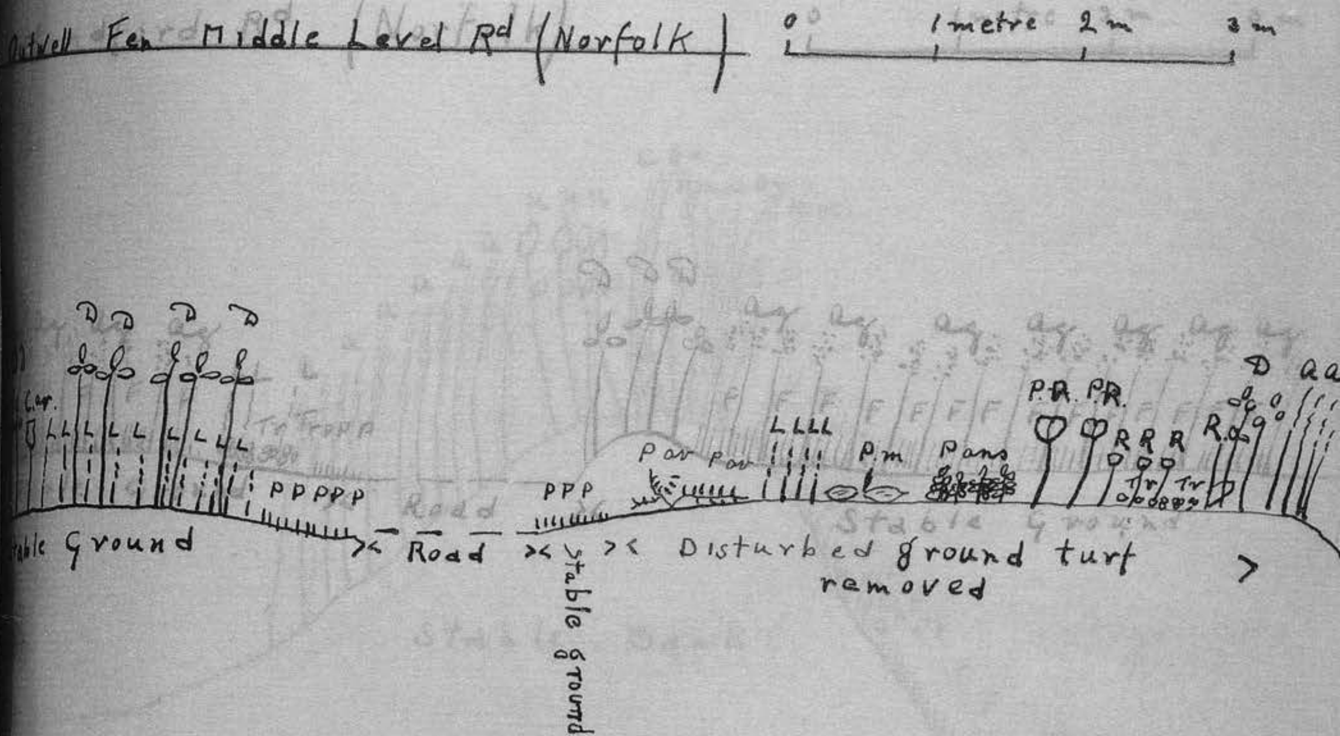



Trans 5
Stoke Ferry Rd (Norfolk)
0 1 metre 2 m 3 m
Hedge Trimming
Stable ground
Road
Stable ground
Disturbed ground
Channel


Trans 6
Stoke Ferry Rd (Norfolk)
0 1 metre 2 m 3 m
Hedge refuse
Stable ground
Road
Stable ground
Refuse
ground

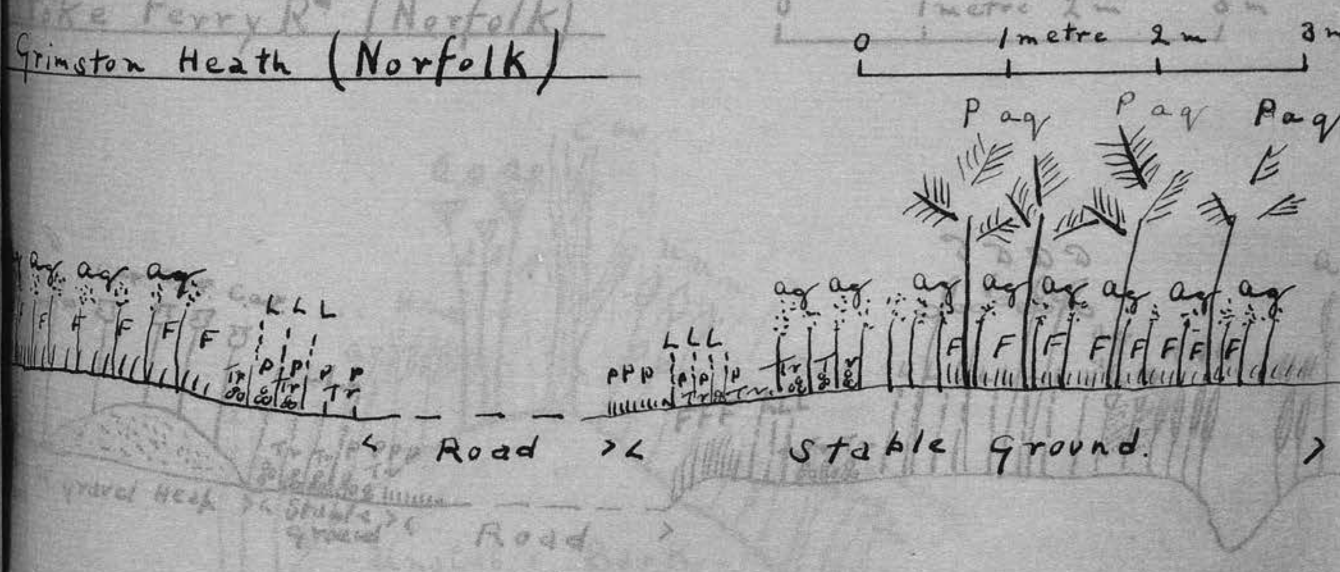
Trans. 7.

Outwell Fen Middle Level Rd (Norfolk)



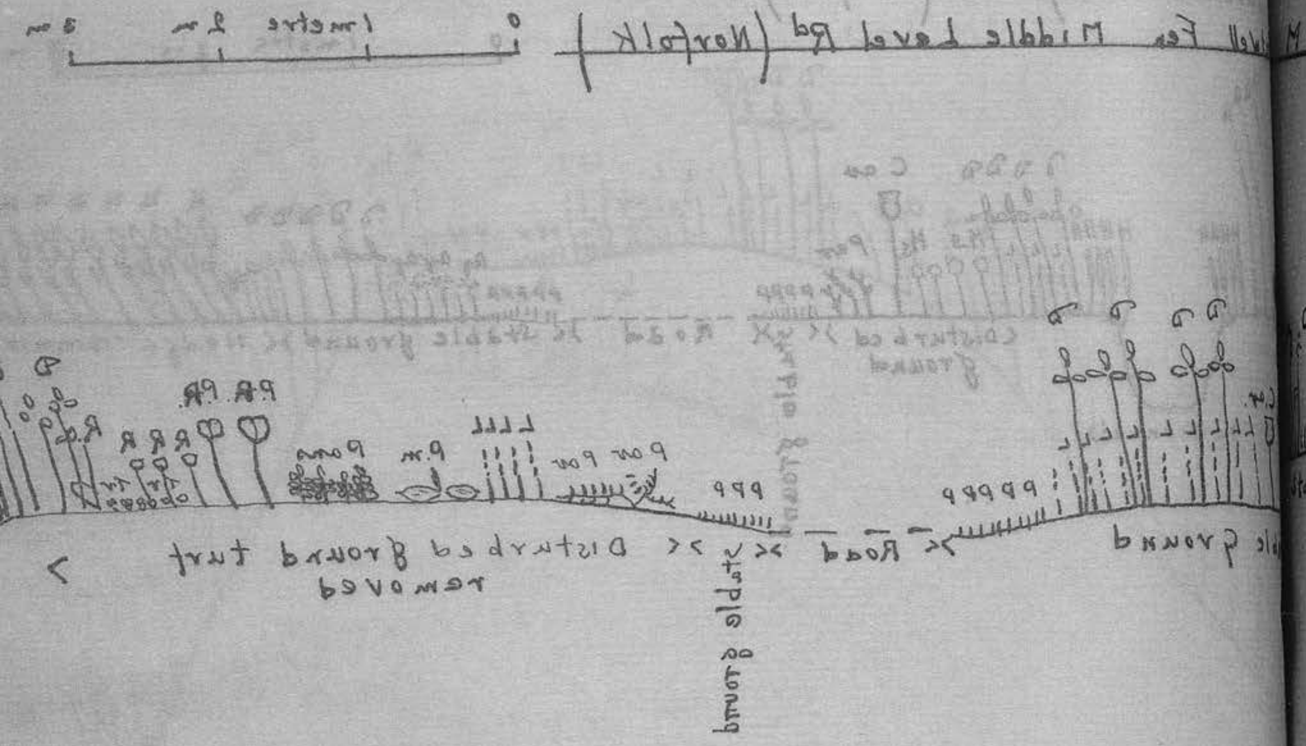
Trans 8

Grimston Heath (Norfolk)



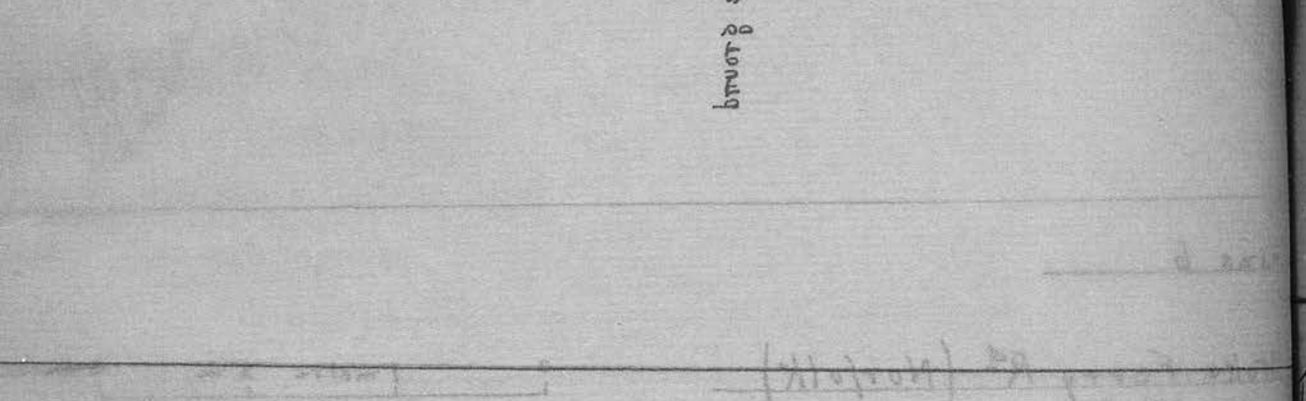
Trans. 7

...well Fen Middle Level Rd (Norfolk)



Trans 8

Grimston Heath (Norfolk)

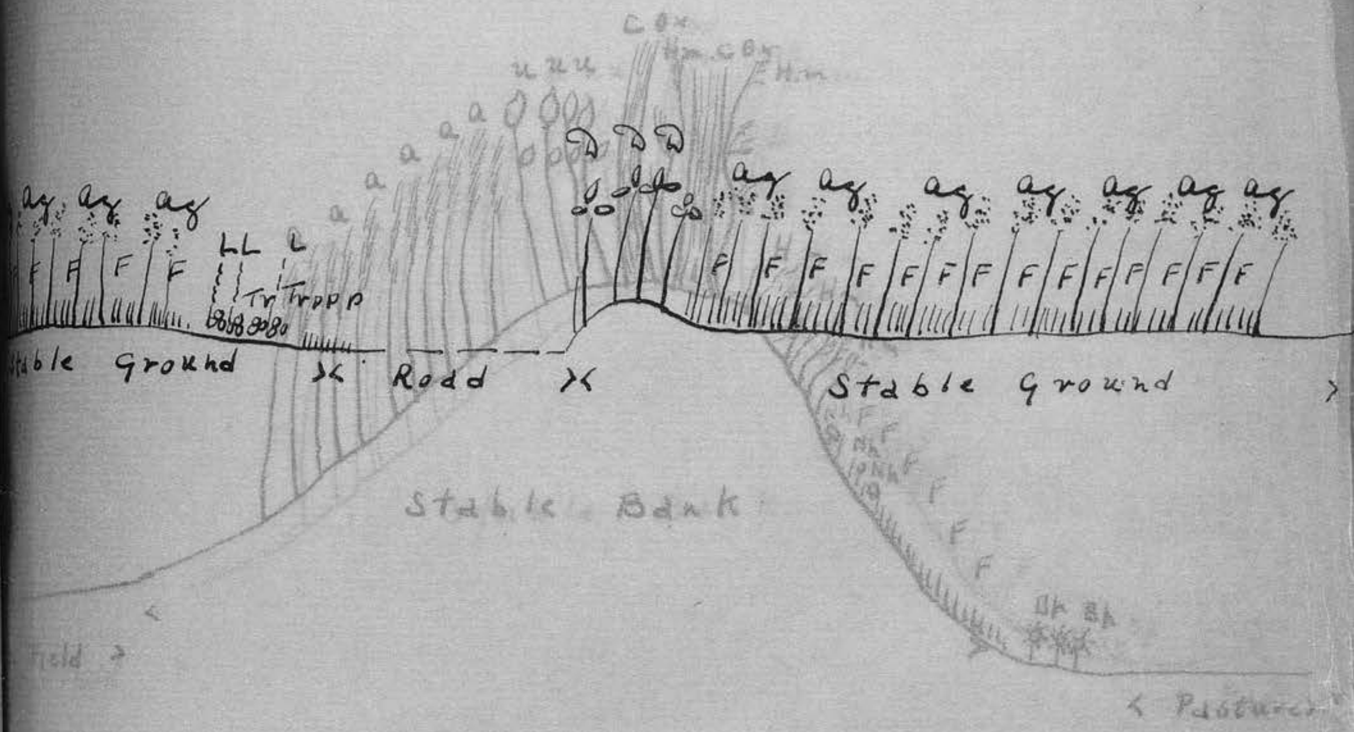


Trans 9

11 Shrowston (Norfolk) 0 1 metre

Mundford Rd (Norfolk)

0 1 metre 2 m 3 m

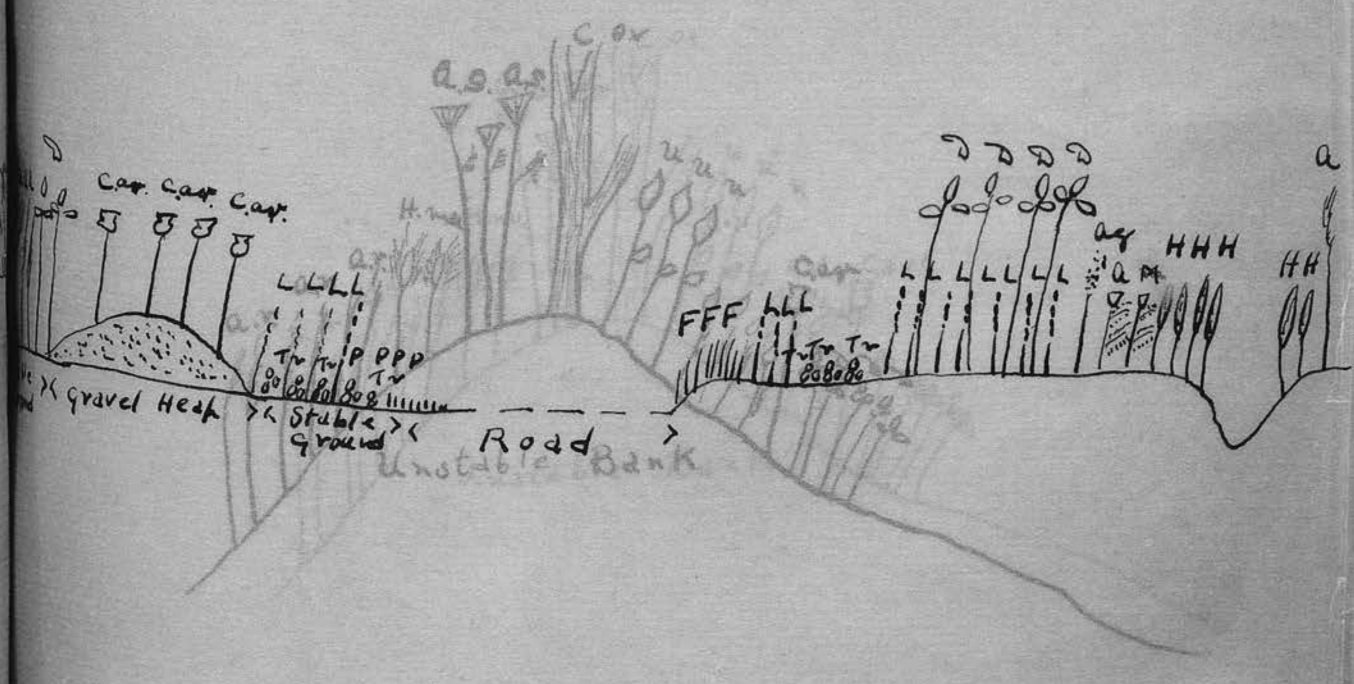


Trans 10

12 Gaywood (Norfolk) 0 1 metre

Stoke Ferry Rd (Norfolk)

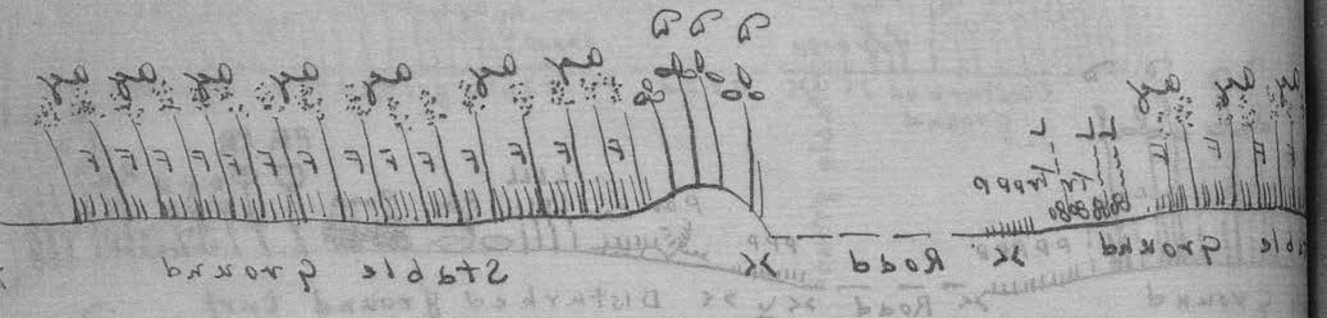
0 1 metre 2 m 3 m



Trans 9

…andford Rd (Norfolk)

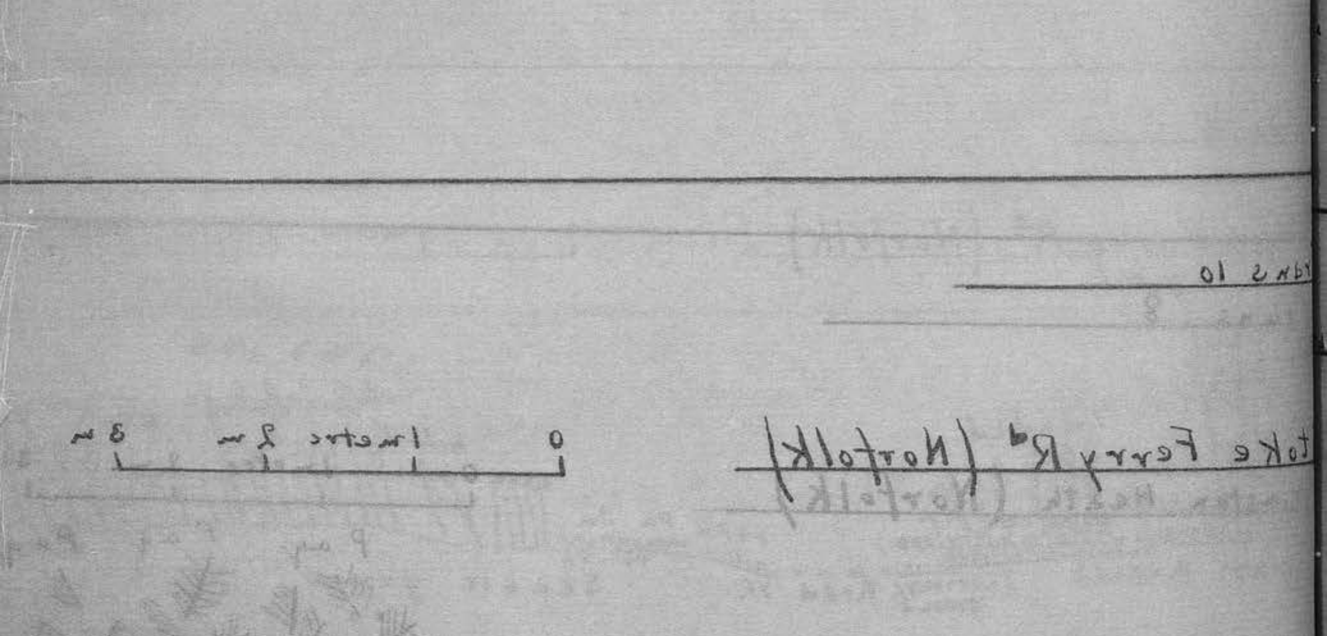
0 1 metre 2 m 3 m



Trans 10

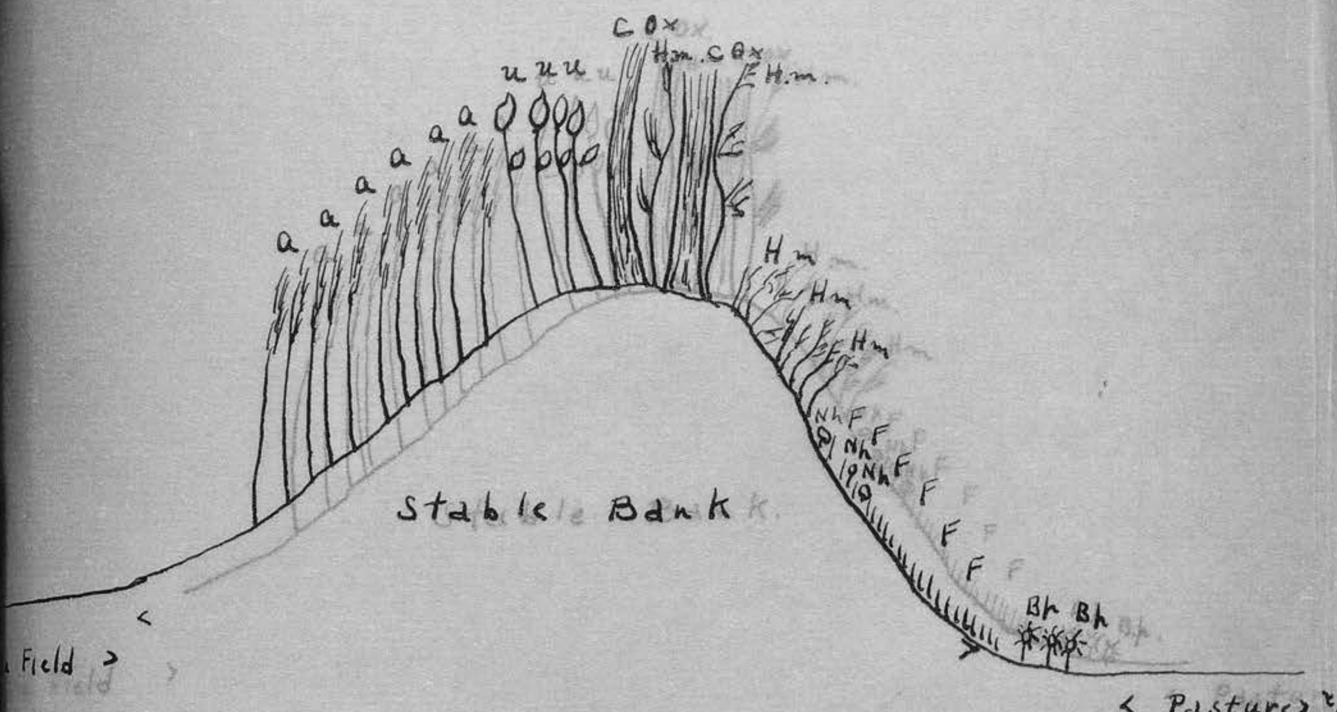
…toke Ferry Rd (Norfolk)

0 1 metre 2 m 3 m



ans 11 Sprowston (Norfolk)

0 1 metre

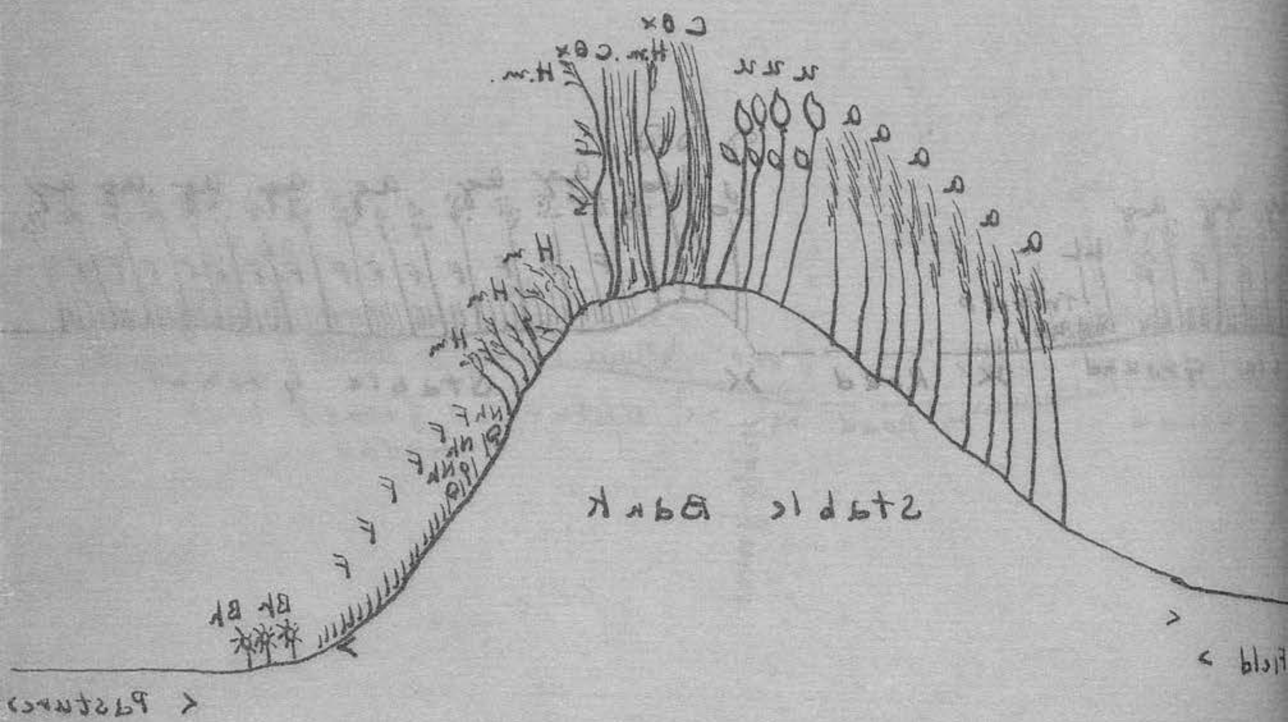


ans 12 Gaywood (Norfolk.)

0 1 metre.

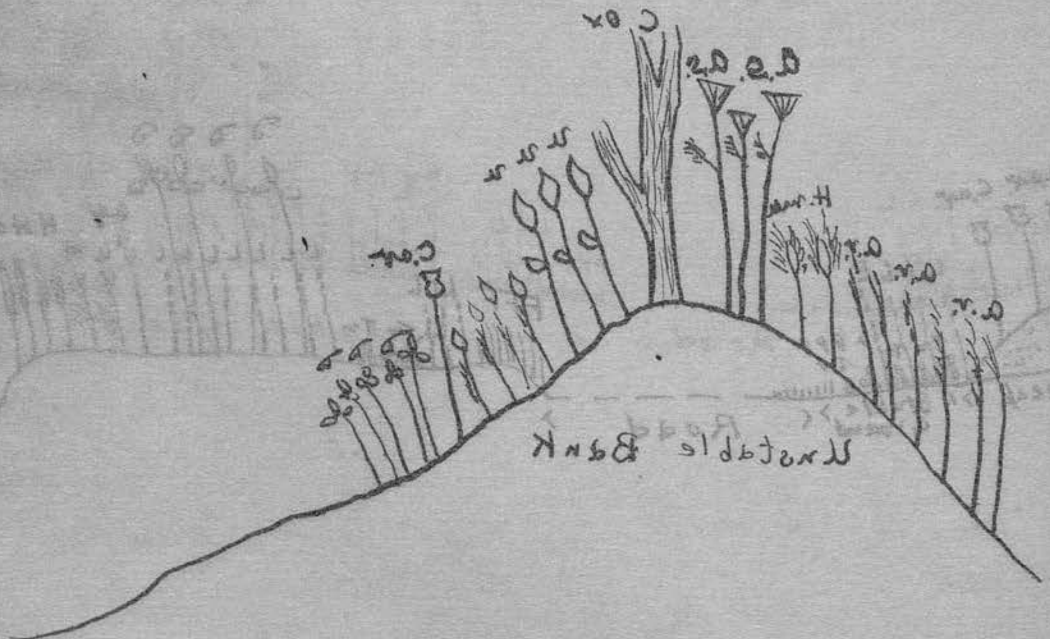
11 Sprowston (Norfolk)

0 1 metre



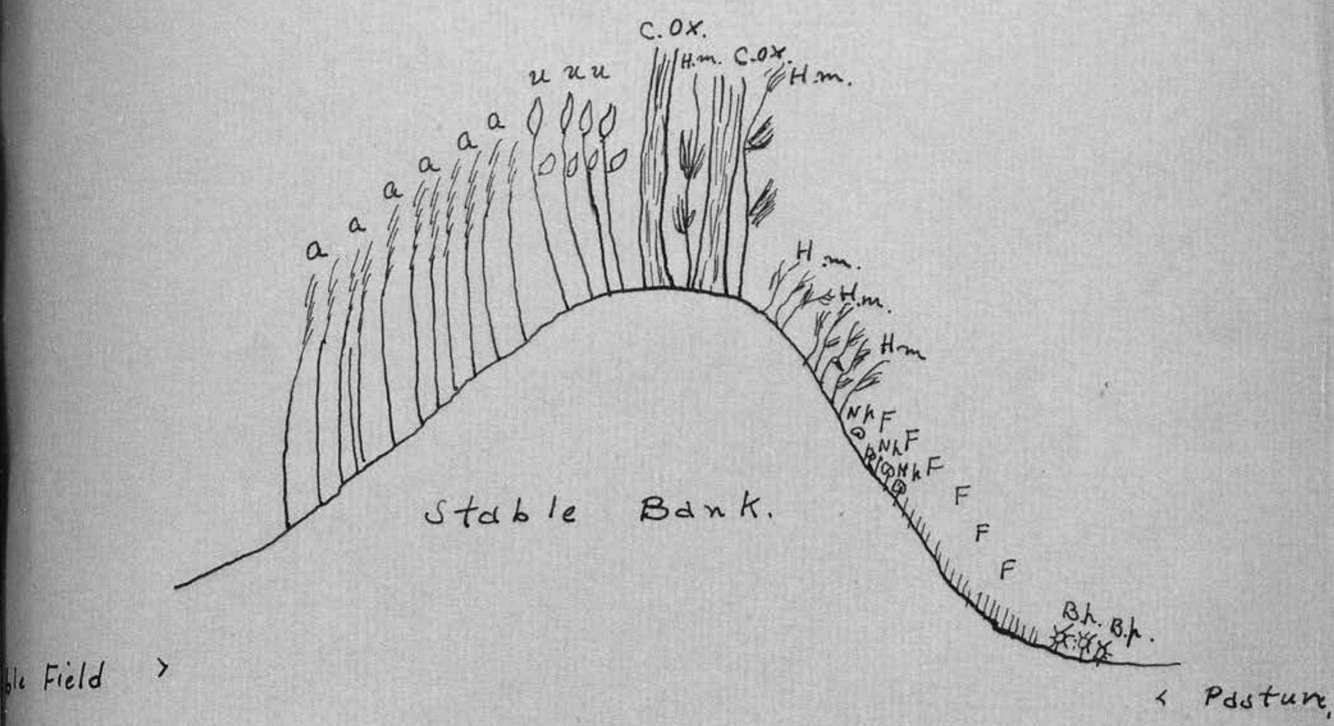
12 Gaywood (Norfolk)

0 1 metre.



Trans. 11. Sprowston.

0 1 metre



Trans 12. Gaywood

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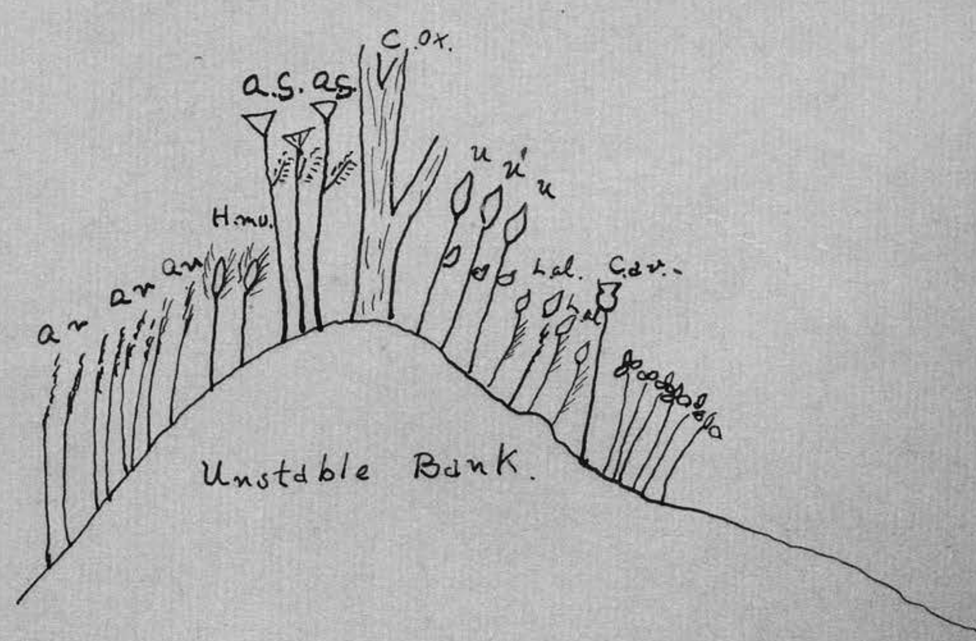

SECTION

6

THE DISTRIBUTION OF THE CREEPING THISTLE

(*Cirsium arvense*)

THE DISTRIBUTION OF THE CREEPING THISTLE. (Cirsium arvense)

THE DISTRIBUTION OF THE CREEPING THISTLE (Cirsium arvense)

The Creeping Thistle (Cirsium arvense) is a very characteristic plant of semi-natural vegetation, and of cultivated land. As a species it is scheduled as an injurious weed under the Injurious Weeds Order, and its detriment to agriculture needs no elaboration. A study of the distribution of this plant and the factors influencing it, is of interest from the ecological and from the economic point of view.

Agriculturists regard colonies of Cirsium arvense as an indication of fertile soil, especially when the individuals are numerous and vigorous.

In Raunkiaer's system the species would be classed as cryptophytic, being a "root bud" geophyte.

Cursory observation shows the following situations to be the most common, bare ground which owes its origin to human activity, eg. bare patches at the way-side and the heaps of earth which result from any engineering operations. Heaps of stone, gravel or sand at the roadside are frequently dominated by Cirsium arvense, though the plant may not be abundant in the surrounding grass. Steep banks where bare earth is exposed owing to subsidence or the sites of land-slides or quarry workings are often covered with dense colonies. Bare sandy patches on heath land may possess Cirsium arvense as the only vegetation, and the same applies to much of the derelict light arable land, in spite of the fact that the species is regarded as an indication of fertility.

The following sites also have been instanced,

See Appendix at end of Section.

(15) "A manure heap, a fire puddling and thus producing bare areas, poaching the ground rather late in the spring, foddering and even liming, will give thistles a run for several years, even if there were apparently none before.

On much arable land in the Midlands there appears to be something about the time or the method of potato cultivation that induces thistles to persist for several seasons. Hoeing in roots in May and early June will bring up six for one, but in wheat at the same time hoeing will, with the competition for light, stop it from getting in front again."

In crops of Clover, Lucerne, or Sainfoin, Cirsium arvense may be abundant, but diminishes when a sward of grass forms. It is upon pastures that the species is most frequent and abundant and gives most trouble to the agriculturist, necessitating special mowing operations. On meadow land, e.g. grass land which is mown each season for hay, the plant is less abundant than on pasture land. The problem of distribution on the two latter situations receives special consideration in this work.

1. Distribution on Arable land, Waste places, etc.

Bare Ground: The population of bare ground by Cirsium arvense is, when it does occur, very rapid. The invasion of the area is by underground runners from the surrounding earth where probably only a few suppressed individuals exist. *On a certain roadside only 43 individuals were noted in a distance of 300 yards. Soil was deposited in the shape of a bank during winter, and in the following summer about 800 individual shoots were counted.

Vegetative spread is extremely rapid and it is well known how the plant spreads by horizontal underground runners or stolons, sending up shoots at certain intervals. Sometimes the shoots spring from the horizontal runner forming secondary roots, but no tap root below the runner. At certain intervals along the runner a shoot will be found

* Massingham Norfolk. This is a common phenomenon

possessing a very deep tap root. A shoot may give rise to a horizontal underground runner at a higher level than the original. Under unfavourable conditions the runners appear to be capable of quiescence for some years.

Rapid vegetative spread probably accounts for the popular belief that distribution and reproduction by seed does not occur.

It is worthy of note, particularly in connection with a latter part of this investigation, that heaps of material or molehills exert no stimulus on the species when occurring on bare ground.

Several reasons may be advanced for the stimulus exerted by bare ground on the runners. Light, moisture and plant food are the most probable factors concerned, together with absence of competition by virtue of the bare condition of the ground.

<u>Heaps at Road-sides</u>: During summer months most roads are lined by heaps of stones, gravel or sand, for various operations. The domination of many of these heaps by Cirsium arvense is very striking (Figs. 111,112,113). Examination shows that, even on the top of heaps, the shoot may be traced vertically downwards to the underlying earth and thence to a horizontal runner. Sometimes secondary horizontal runners may be formed in a deep heap. Fig. 114 shows a heap 8 ft. high in a quarry where the above phenomena were noted. The colonisation of the heap may occur when only one or two plants are noticeable in the surrounding grass.

After the removal of the heap a fresh crop of plants arises on the piece of bare ground left, (Fig. 115) but the invasion of the area by grasses reduces the number in the following year, thus in the example illustrated by Fig 115, only three weak individuals occurred the following summer. It has been found however that a few individuals may still mark the site of a former colony for two or three years, after the disappearance of the heap.

Banks: Cirsium arvense occurs frequently upon banks when bare soil is exposed, e.g. where subsidence has occurred as on any steep bank. In this case the plants may be traced by their runners as arising from underground parts of individuals growing at the top of the bank. It is only upon the bare soil where the subsidence occurs that Cirsium arvense appears.

Sandy Land: Despite the belief that Cirsium arvense is an indication of fertility, this species often grows abundantly and with vigour upon poor sandy land. In several instances strong colonies have been observed on derelict arable fields on sandy East Anglian heaths. The soil was so poor as to carry only a 25% cover of weeds and these were ripe and withered in the month of June.

On certain heaths covered mainly by hummocks of heather (Erica cinerea), bent (Agrostis spp) and sheep's fescue (Festuca ovina) which are surrounded by larger areas of bare sand. The shoots of Cirsium arvense were observed only upon the bare sand, and not in competition with the heather or grasses (Fig. 116)

Arable land: The presence of Cirsium arvense on arable land needs no substantiation, especially in the case of cornfields. In root crops the plant is usually suppressed by surface cultivation and by the fact that the crop is drilled or planted later in the season than is the case with cereals.

Observations on cereal crops have shown that the shoots of Cirsium arvense arise early in spring when the ground is only partially covered. Counts taken in ten cases showed that 84% of the total number of individual plants of Cirsium arvense occurred on the bare ground between the rows of cereals. The distance between the middles of any two rows of the cereal crops was 6" to 7", the young plants of the cereal occupying 1" - 2" of this at their base. Of these plants of Cirsium arvense growing in the lines of drilled cereals 66% were found growing in the gaps due to faulty drilling. The shoots which appeared actually among the growing cereals were in some cases thin and weak, but in other cases the plant bent outwards sharply at a distance of about 6" from the ground and then continued to grow directly upwards.

Discussion of Influencing Factors

One striking fact appears from a consideration of the above habitats, and that is that the species prefers bare ground to that covered by vegetation. When ground is exposed through any agency or when heaps of fresh earth, stone, gravel or sand are deposited, the area may be rapidly occupied by runners of Cirsium arvense, and shoots arise in large numbers at an extraordinary rate.

The bare area appears to exert a strong stimulus upon the underground vegetative organs of the plant which originate probably from one or two suppressed individuals in the vicinity. Though only one or two individuals may exist in the first place, it is of course impossible to estimate the size and extent of their underground organs without resort to excavation.

It is difficult to determine at first sight whether one or more factors are responsible for the phenomenon and several possibilities arise. The influence may be plant food, freedom from plant toxins, light or moisture.

The influence of plant food is ruled out by the frequence of the species upon heaps of stones or gravel. There is no reason to suppose that the shoots should find difficulty in forcing their way through a turf, in fact there appears no evidence of this disability.

Light as a factor demands attention as the evidence of the behaviour of the plant in cereal crops points to the attraction of unshaded areas, and the plant's affinity for light. Later in this work reference is made to the suppressing influence of tall grasses.

It is difficult to see how an illuminated area can exert a stimulus upon shoots arising from buds situated upon deeply buried horizontal runners, so that while light may be of vital importance when the shoots have emerged from the earth, it is not likely that this factor is responsible for their invasion of the area concerned.

All the habitats under consideration have one character in common, i.e. a freedom from grass competition. The toxic influence of a sward of grass roots is well known. CO_2 is more abundant in the soil air under a grass turf than under arable conditions. (37) Russell and Appleyard (1915) record 9.1 % CO_2 in a wet moor sod near Rothamsted. Carbonic acid concentrations of 1 % to 2 % have a toxic influence for many plants. (J Braun-Blanquet. "Pflanzensoziologie")

* It is quite obvious that a bare surface admits moisture more readily and that the earth under heaps is moister than that of the surrounds, but it is difficult to see how this can influence a species with such a deep and extensive root system.

It appears from the above considerations that freedom from the influence of grasses is responsible.

In cases where it is possible for grasses to invade a bare habitat, the colonies of Cirsium arvense rapidly diminish and in a year or two may disappear entirely.

Distribution by seed.

It has been shown in the laboratory in a recently conducted investigation that seeds of Cirsium arvense may have a germinating capacity averaging 12.6%

(16) If this is maintained in nature, all the habitats mentioned above would appear to be potent sources of infection to the countryside, but the fact remains that it is a very uncommon occurrence for seedlings to be found, and of many hundreds of cases examined by the writer all the individual shoots, noted in early spring while in the small stage, had arisen vegetatively from old deep seated runners. In all the cases the remains of the shoots of pre-existing individuals, though sometimes few in number, could be found.

It has been stated that Cirsium arvense seeds and germinates in autumn, in some cases, and that the seedlings may make sufficient root system for subsequent growth, after frost has killed the foliage. Searches conducted

*See fig: 117

by the writer throughout all seasons of the year have failed to discover a single example of this phenomenon. Shoots which appeared to be seedlings would upon e xcavation prove to have arisen from an old runner.

On the other hand it must be admitted that the population of reclaimed land by Cirsium arvense (e.g. Crown lands bordering the Wash)- can only be by seed infection. On the areas considered in this work, however, vegetative reproduction appears to be the only mode of proliferation worthy of serious study.

II. Pastures and Meadow land.

The distribution of Cirsium arvense upon pasture and meadow land constitutes a problem in itself and one of major importance from the agriculturist's point of view. The following notes are a record of observations carried out in an attempt to determine the influencing factors.

In the previous pages it was clearly seen that all sites occupied by the species possess one factor in common, i.e. a bare surface or a surface which was recently devoid of vegetation. The connection is so constant and patent to the observer that one looks for similar phenomena in the case of permanent grass land.

On the densest of grass land, and on that covered by a "mat", bare patches may occur from a large variety of causes. Cart ruts, puddling by cattle and horses, human activities of various types, all produce bare ground. The deposition of rubbish and other material may produce the same effect as the heaps at the road side. While these areas are usually occupied by Cirsium arvense, they form such a small proportion of the whole that they cannot be held responsible to any appreciable extent for the wide-spread distribution of the species over the large tracts of grass land which it occupies.

An investigation was carried out to determine whether any explanation could be found. After numerous surveys a very striking fact came to notice and that was the almost constant association of colonies of Cirsium arvense with mole-hills. An examination was made by the writer of 100 cases of the occurrence of Cirsium arvense on permanent grassland. In all the examples the disturbing influences enumerated in the previous paragraphs were absent. It was found that in every case mole activity was present.

A survey was made on Massingham Heath in Norfolk on pastures at Boughton and Stoke Ferry and on Brisley Common, a total of some thousands of acres. Mole activity occurred upon small detached regions of these places, and upon these regions the only colonies of Cirsium arvense were found.

It was noted that in many cases the grouping of the plants round a mole-hill exhibited an appearance similar to that noted on road-side heaps,(Fig.118). It was also noticeable that the regions of most intense mole activity, i.e. regions shewing the most mole-hills, also possessed the largest number of plants. To obtain data regarding this latter co-relation an intensive survey was carried out in the following manner. Transects 100 metres long by 1 metre wide were taken through colonies of the species. The number of mole-hills within the transect and also the number of thistles were recorded.

Five colonies were chosen and four transects made through each, i.e. twenty transects in all.

The results are tabulated below

TABLE XIV

	Transects 100 m. x 1m.	Number of Molehills.	Number of plants of Cirsium arvense
1.	Massingham	26	51
2.	"	58	60
3.	"	99	184
4.	"	81	193
5.	"	32	47
6.	"	46	63
7.	"	61	94
8.	"	61	102
9.	Boughton	18	6
10.	"	69	54
11.	"	42	45
12.	"	54	84
13.	Brisley	63	112
14.	"	92	72
15.	"	14	25
16.	"	8	17
17.	Fincham	109	187
18.	"	160	192
19.	"	46	86
20.	"	73	98

The above co-relations are represented graphically in Graph 1.

GRAPH 1

*The location of the plants upon or on the margin of the actual mole-hill appeared to exist in the case of the majority of shoots observed in early spring. After surveying twelve transects, each in different colonies, it was found that of a total of 408 shoots, 195 occurred on the mole-hills or their margin, i.e. 48% of the total. In addition it must be noted that approximately only 26% of the ground was covered by mole-hills, and further that about 10% of the hills were of very recent origin.

It must be borne in mind that after the appearance of a plant upon a hill the evidence of the existence of the hill may soon be obliterated. The operation of chain harrowing in spring often destroys all trace of the mole-hills. In the case of certain grassland communities the other species comprising the sward may soon dominate a mole-hill, and if the latter has been flattened by rain all evidence of its existence may disappear. Species bearing surface runners, such as wild white clover (Trifolium repens), may soon invade the surface of the hill while bent (Agrostis spp) and buttercup (Ranunculus spp) may force their way up from beneath.

It was noted in the case of the roadside heaps that plants of Cirsium arvense appeared in decreasing numbers for two or three years after the removal of the heap, and the covering of the area by grass. This also may explain the appearance of plants not in actual contact with the surface of a mole-hill.

It would appear that the influencing force exerted

* This phenomenon has been noted also in pastures in Wales. (39)

by the mole-hill is that of a bare surface as in the case of the road side heap. On a dense sward or matted turf the moister state of the earth under the mole-hill in comparison with that of the surrounds is obvious to the eye, but this is not so marked on an "open" turf.

The activity of moles is related to the abundance of earthworms, the chief component of their diet. Earthworms in their turn prefer the soil richest in organic matter with a good water supply coupled with free drainage, in other words the most fertile ground. This may explain the traditional association of thistles with soil fertility on old established grassland.

*It is well known that Cirsium arvense is less abundant on land where the grass is allowed to grow for mowing. This is stated to be due to the fact that the overshadowing effect of the grass causes the plants to grow taller, with leaves further apart on the stem and lower leaves further from the ground. When the hay is cut the portion of the stem left in the ground is devoid of leaves and dies in consequence(17).

†On the other hand in horse paddocks, and pastures heavily grazed by horses Cirsium arvense does not appear on the grazed patches, but always grows abundantly among the

+ On the other hand Cirsium arvense is more abundant where Trifolium repens dominates a pasture. In this case the grasses are suppressed and as T repens is deep rooted, the turf is "open", there being freedom from a mass of roots at the soil surface. There is a larger proportion of exposed earth.

The above phenomenon is well illustrated on the Cambridge University Farm. Experimental strips of grass mixtures have been sown, including two strips containing T. repens only. On the latter strips grasses are almost absent, the plots are more heavily grazed than the grass plots and there is a higher proportion of bare ground.

On the T.repens plots there is a great abundance of C. arvense with a striking demarcation from the grass plots where Cirsium arvense is comparatively scarce.

† See appendix.

rank grass where the horses dung, and do not graze. (For an account of the influence of horses on grass land, see Section 10 page 176). It is noteworthy that mole-hills are very abundant upon these ungrazed patches and scarce on the grazed patches, though the mole-hills on the former site may be obscured by the long grass.

The dung attracts earthworms and larvae which attract moles, thus producing mole-hills, and consequently Cirsium arvense asserts itself.

Prevention and Eradication

It is not asserted that the cutting of thistles to prevent seeding is useless, but the fact that seedlings occurring in a state of nature are rarely discovered does point to the propagation of the plant by seed as being of minor importance in comparison with vegetative spread.

All practical methods possible must be employed to check vegetative propagation. Chemical destruction of the roots with a 15% solution of sodium chlorate during a period when the land is not under cultivation, is said to be a reliable means of eradication. This together with frequent cutting of the shoots might be employed in waste places as well as on cultivated land during bare fallow.

On grass land frequent cutting is still considered the best means of eradication, but in view of the above investigations the frequent harrowing down of mole-hills together with the trapping of the moles is worthy of serious consideration.

Conclusions

The chief means of propagation of Cirsium arvense is vegetatively.

A stimulus to vegetative reproduction is afforded by the absence of grass competition, and it's toxic influences due to exhalation of CO_2 by a dense mass of roots.

Sites where grass competition has been removed e.g. certain arable cultivations, sites of engineering operations, earth subsidences, gravel or sand heaps and bare sand devoid of other vegetation, etc. are frequently colonised by Cirsium arvense.

On pasture and meadow with a turf which is dominated by Trifolium repens or where the turf is "open", i.e. not covered by a dense mass of roots, C. arvense may occur by virtue of this condition.

On densely covered grass land, such as old established pasture, any disturbing influence such as puddling or heavy spring grazing, which breaks the mat and exposes bare earth, will stimulate the proliferation of C. arvense.

In the absence of any of the above disturbing influences upon dense or matted grassland the activity of moles, in the form of molehills, is the responsible agent.

OVER

APPENDIX.

Since completing this work a communication has been received by the writer from Mr. Martin G. Jones of the Agricultural Research Department of the Imperial Chemical Industries Limited. Jealotts Hill, Bracknell, Berks.

The following observations were made upon the invasion of land laid down to grass for experimental grazing plots, which have now been in existence for three years.

(a) Perennial Ryegrass (Lolium perenne) has shown a striking suppressing influence upon C. arvense. The following figures have been communicated to the writer by Mr. Jones.

"When the plots had differential seeds sown the following number of thistles (C. arvense) were found per 80 square feet.

Plots sown with Perennial Ryegrass.........-	22
" " " Rough stalked meadow grass.-	351
" " " Crested Dogstail...........-	360
" " " Wild white Clover..........-	143
" " " Seeds mixture including Perennial Ryegrass.......-	15

The above figures appear to be significant.

(b) "Where the same seeds mixture consisting of Ryegrass, Rough stalked Meadow Grass and Wild White Clover had been sown and then plots marked out to get differential grazings, two plots each were overgrazed in the spring and undergrazed in the summer and autumn. This way allowed the thistle to get in more quickly, that in three years time it had a distinct hold whereas the remaining six plots which had not been overgrazed in the spring nor been undergrazed in the summer remained practically free".

In the plots which were overgrazed in spring and undergrazed in summer and autumn there were 25 thistles per 80 square feet in one plot and 12 per 80 square feet in the other plot, whereas in the six plots which were not overgrazed in spring and undergrazed in summer and autumn there were 1,5,0,0,0,0 respectively per 80 square feet.

From the above observations it would appear, in the writer's opinion, that the suppressing influence of Lolium perenne may be due to the fact that this grass is characterised by its vigorous vegetative development in early spring when other species are still practically dormant, and from its "winter green" condition. * The species would thus present competition and exert a toxic influence in the early part of the year.

Rough stalked Meadow Grass (Poa trivialis) is later in season in exhibiting development and is less "winter green". Crested Dogstail (Cynosurus cristatus) is very slow in establishing itself even when sown in pure culture. Wild White Clover (Trifolium repens) still shows a high proportion of thistles in comparison with Lolium perenne.

The increase of C. arvense by early spring grazing would, in the light of foregoing conclusions in this Section, be due to the suppression of grass competition in early spring, when the thistle shoots are emerging.

* Parker's experiments (1924) indicate that different species release different quantities of CO_2. (J. Braun-Blanquet. "Pflanzensoziologie".) This may provide an explanation.

The absence of C. arvense from areas closely grazed by horses may, in the light of the above observations, be explained by the presence of Lolium perenne on the grazed areas in large proportions, and its absence from the ungrazed patches. Tables XXVIII & XXIX Section 10, page 177 show 30% and 33% Lolium perenne respectively on the grazed areas, and its absence on the ungrazed patches.

Fig.111. Cirsium arvense and Agropyrum repens invading stone heap. (Clipstone,Norfolk).

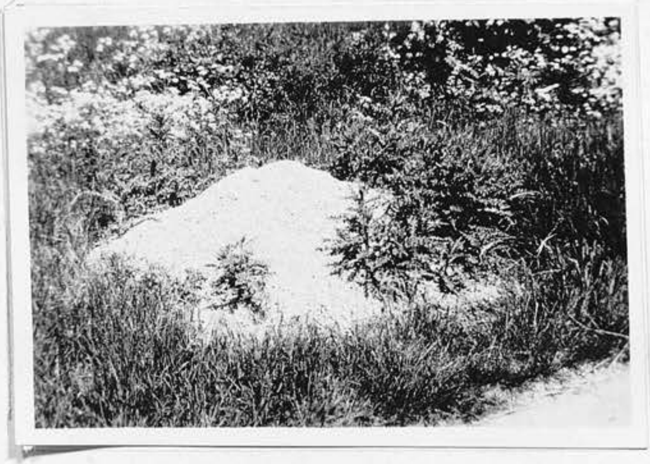

Fig.112. Cirsium arvense invading gravel heap. (Northwold,Norfolk).

Fig.113. Cirsium arvense dominating sand heap. (Massingham Heath,Norfolk).

Fig.114. Cirsium arvense dominating gravel heap.8ft high. (Crimplesham Norfolk).

Fig.115. Cirsium arvense on site of recently removed gravel heap. (Terrington St.Clements,Norfolk).

Fig.116. Cirsium arvense populating bare sand (Wooton,Norfolk).

Fig.117. Zone of dense dark green grass around margin of sand heap on dry grassland. (Knight's Hill, Norfolk).

Fig.118. Cirsium arvense invading mole-hill (Massingham Heath Norfolk).

SECTION.

7.

THE DISTRIBUTION OF THE STINGING NETTLE
(*Urtica dioica*)

THE DISTRIBUTION OF THE STINGING NETTLE (Urtica dioica)

∅ THE DISTRIBUTION OF URTICA dioica

The common stinging nettle Urtica dioica is the most characteristic species of semi-natural vegetation as a whole. An atmosphere of mystery has always surrounded the presence of this species, as it appears to spring up in immediate association with human habitation or activity. By most botanists it is regarded as a nitrophilous species and has become the common text book example of this type of plant. The non-scientific observer appears to have associated nettles with nitrogen as they are regarded generally as a sign of high fertility.

From the economic aspect the distribution of the plant demands attention, for it is a serious weed in agricultural practice. Up to the present time methods of eradication have not been based upon any scientific investigation as to the life form or mode of proliferation of the species. Chemical applications or simple mowing down of the colonies have been the only agents employed in their destruction.

It is necessary to distinguish Urtica dioica from Urtica urens. The latter is a therophyte in life form and not a characteristic species of semi-natural vegetation as it occurs chiefly on arable land.

Urtica dioica may be classed in Raunkiaer's system of life forms as a hemicrytophyte and further described as

∅ Accepted for publication (with slight amendments) by the "Journal of the Ministry of Agriculture."

Published . Jan. 1933. Vol. XXXIX. No 10. page 912.

See Appendix at end of Section.

a protohemicryptophyte B, with creeping offshoots, stolons or rhizomes, (see Section 1 page. 6.)

Lamium album, as already remarked, has an exactly similar life form to Urtica dioica though it belongs to a different natural order. Owing to this similarity of life form it is rarely found out of association with Urtica dioica and occupies the same type of habitat, the two species forming a synusia.

The influences stated to affect Urtica dioica may, during the course of this work, be taken as applying also to the problem of the distribution of Lamium album and also within the limits of its less wide distribution to Aegopodium Podagraria, a species of practically similar life form. In the latter case the runners are at soil level or just below, while in the case of Urtica dioica or Lamium album they are more frequently on the soil surface, but below some loose covering material. This loose surface cover also characterises the habitat of Aegopodium Podagraria, and Mercurialis perennis.

Primary Survey and Investigation

Nettles are never common on heavy clays to the extent to which they are found on lighter soils. Their abundance in the fens, where the soil is unusually light, has augmented the "nitrophilous" theory, but on the other hand they they are equally abundant on light silts or the notoriously infertile Lower Greensand heath lands.

Apart from the appearance of the species in grass fields, a subject discussed later, there are many common sites almost too familiar to need description. Hedgerows and banks are almost constantly marked by belts and colonies of nettles as are also the margins of ditches, though to a lesser extent. Woodlands, heaps of timber or peasticks shelter the plant which appears to be adaptive to light or shade, though often aetiolated in the latter case. Buildings both of stone or wood, whether temporary or permanent or in a derelict state, are usually fringed by nettles, and the plant will persist and mark the site of habitation long after all traces have vanished, and the foundations are hidden beneath the earth. It is this latter phenomenon which has given rise to the mystic association between the plant and human beings.

Heaps of stone, gravel or sand, frequently become covered with nettles and after the heap is removed, the colony will usually become established.

Rabbit burrows are often marked by nettle colonies, a fact noted by Farrow (18).

*. A survey of the above sites, in various parts of the country, soon led the writer to question whether the nitrogen content of the soil had any bearing whatever upon the presence of the plant. In view of this, other possible explanations were sought, and it was when examining the structure and arrangement of roots and runners in a nettle colony that a key to the problem was found.

The first colony to be investigated in this way was a small one of apparently two years duration, on a shingle beach above high water mark (Bardsea. N.Lancs). Fig.119

* The coincidence of rich growths of Urtica dioeca with the inherent capacity of the soil for nitrification is claimed by Olsen (33.): This may refer to luxuriance of foliage more than to actual presence. The same might be claimed of numerous species. The nitrifying Urtica soils are also comparatively rich in phosphoric acid which may affect luxuriance (cf. Braun-Blanquet. 'Pflanzensoziologie')

shows the central stock of last years plant, with runners radiating therefrom. Each runner bears a newly established plant at its extremity. It was noticeable that the runners worked their way through crevices between the stones, at a depth of about one to four c'ms below the surface. The root system was very shallow as is the case in all colonies. The position and relation between roots and runners is shown in Fig.120. Each new plant sends out a fresh runner which always appears limp and lacking in penetrating power, Fig.121.

When the runners were exposed they turned black and died, in cases where the exposure had caused injury. The cause of death appeared to be desiccation. Where the runners were uninjured they did not die but their buds sprang into leaf, apparently prematurely, for further proliferation ceased and the resulting shoots were stunted and weak in appearance.

The fact is very evident that the runners cannot tolerate exposure, and must have a surface covering to prevent premature opening of buds, and the check to proliferation. At the same time the runners are unable to force their way through any resistant material, as will be shown later.

That light is a more inhibiting factor than desiccation would appear to be indicated by the following observations. When wooden floors, raised two inches from the ground, were laid alongside patches of nettles, the runners spread under the platforms to the other side, a distance of five feet. Light was excluded at each end by the grass, the covered area being in total darkness. At the same time the soil surface, along which the runners spread, was dry and dusty. When glass frames were laid on the ground, the runners did not grow under them, apparently owing to the light.

It remains clear that the runners require a surface covering of some loose but sheltering material as essential for their development. It is hoped in the following exposition to demonstrate that it is the presence of this loose cover which explains the establishment and spread of nettles, in all cases. In other words a mechanical and not a chemical factor.

J Braun-Blanquet, ("Pflanzensoziologie") mentions the following species as indicators of nitrifying power of the soil in woodlands :- Rubus, Galeopsis, Fragaria, Epilobium augustifolium, Mercurialis perennis, Asperula and Paris.

It appears highly significant to the writer that these species occurring in the loose litter of the woodland floor, are, with the exception of Galeopsis, all possessed of the creeping type of rootstock.

Galeopsis can only be described as an occasional in woodlands.

Discussion of Common Sites.

Hedgerows Nettles are probably the most common plant of the actual base of the hedgerow, particularly on the lighter soils. In the actual hedgerow itself they may completely dominate all other vegetation. It is the base of the hedgerow which the hedger finds almost impossible to keep clean, and which consists of a compost of soil, road sweepings, dead leaves, and twigs. This material is light and dry and provides the cover metnioned above. Owing to the large amount of organic matter, the nitrogen content as shown by analysis, is high, but as much of the organic matter is undecayed, it is open to question if there is much available nitrogen.

When the bank is kept clean of surface material, nettles will be confined to the base of the hedge, but any litter or other body kept on the surface will very rapidly become colonised. An investigation of patches of nettles protuding from the base of the hedge will generally provide some clue as to the material which caused their advance. In investigating fifty such patches chosen at random, during excursions along road ways, the writer was able to determine the cause immediately in thirty two cases. Nine further determinations were made subsequently, by enquiring from roadmen and others who remembered some pre-existing cause. In all forty-one cases out of fifty. The remaining nine cases were of old established colonies, and it was reasonable to presume that the cause had been removed beyond trace.

The commonest causes in the above cases are heaps of hedge clippings or of grass mowings from the bank. Stone, gravel or sand heaps are common factors, while such things as tree trunks and heaps of drain pipes have been noted as being responsible, also the pasting of mud and road cleanings on to grassy banks.

Figs.122,123, and 124 show a sequence of events. In fig.122 the nettles were confined to the hedgerow, until the patches of mown grass were left lying in the manner shown. Fig.123 shows nettles appearing from under one of the thick patches. Fig.124 shows the subsequent colony after the litter had been cleared away.

Ditches

Cleanings from ditches thrown on the edge of the bank will cause colonies of nettles. This is particularly noticeable in fen districts where ditch cleaning is an essential and regular feature.

In several cases where nettles lined one side of the ditch, and not the other, it was determined from the occupiers of the land that the cleanings had been thrown only on the side where the nettles occurred.

Woods

Many woods are colonised to a greater or less extent by nettles. For this reason they have been described by some as a shade plant, despite the fact that they are usually aetiolated in shade and grow with vigour in the open. Fig.125 shows nettles appearing through the debris in a wood which always provides a surface covering of loose material.

It appears that the coarser and deeper the debris the stronger and taller the colonies. Thus a heap of sticks gives rise to tall plants, possibly due to the added support, or the struggle towards light. Fig.126 shows a clearing in a wood which has been planted with young poplars. The floor of this cleared portion was thickly covered with branches from the former trees. The nettles are much stronger here than under older trees where the litter is fine, consisting mainly of leaves. A distinct falling off may be seen in the latter situation.

At the back of the clearing a tall patch of nettles may be seen, marking a heap of branches, while at the rear of the shaded area under the old trees, a similar though less tall patch is just discernible, owing to the same cause.

Buildings

The growth of nettles at the base of walls of buildings, particularly in rural areas, has given rise to the theory that the plant is nitrophilous. Frequent reference is found in literature to the effect that the nettles grow round the lairages of livestock, where urine oozes through the wall. It is strange that it has never been remarked that nettles grow with equal vigour, and occur with equal frequency at the base of the walls of barns, cartsheds and other buildings where there is no possible source of excess nitrogen. It will be noted that the roots and runners inhabit the crevice between the wall and the earth or the loose stones of the foundations. Often drippings from the eaves leave a loose layer of surface material, and as in the case of the hedgerow, any litter or covering body will cause the advance of the nettles from the wall.

Stone Heaps

These occur as a result of road making operations, demolished buildings, ruins, quarry workings or landslides, and nettles appear to spring up almost automatically. In this case again, it is the loose surface covering, as with the shingle beach, which attracts the plant, for there can be no possible source of nitrogen in a heap of stones. This explains the association between nettles and human activity, for except in the case of landslides, it is only by human agency that such heaps can occur. The former habitations of man are always marked by heaps of stones.

An experiment was carried out in the following manner. On a patch of grass in a paddock, Fig.127 (Hawkshead Hill N.Lancs) a heap of stones was built, Fig.128. The nearest colony of nettles was in the hedge six yards away, but two suppressed seedlings were found in the grass about two feet and one foot from the heap respectively. The heap was built in July 25th, 1931 and a photograph was taken in the writer's absence on Oct.20th, 1931, about twelve weeks later. This shows the heap completely dominated by nettles (Fig.129).

Rabbit Burrows

Patches of nettles often mark the large rabbit burrows, in warrens and on heaths and banks, Fig.130. Farrow (19) explains the persistence of nettles in these positions as being due to the fact that they are unpalatable to the rabbits, which prefer the heather. This however does not explain their appearance.

One might suppose the appearance to be due to an accumulation of nitrogen at the mouth of the burrow due to droppings and urine, but this is not the case. In the first place rabbits do not foul the mouth of their burrows, and an analysis of the soil in which the nettle roots grew, shewed a very low nitrogen figure, lower than the surrounding soil, owing to the admixture of sand (see page 132).

The explanation again lies in the fact that the sand thrown out by the rabbits forms a light surface cover. In this case one may reasonably enquire as to whether sand deposited by other mechanical means brings about the same result. This is exactly the case.

On Massingham Heath, where the rabbit burrows with nettle colonies were observed, there were two tarred roads intersecting the heath. Sand heaps for tar spraying purposes lined the roads, and most of the heaps were quickly colonised by nettles Fig.131.

Sand and Gravel Heaps

These heaps at the road side are often the cause of a nettle patch near the edge of the road. Sand appears to be more conducive than gravel. In both cases a colony will remain after the heap has been removed, as it has by that time become established in the ground.

An interesting observation was made on heaps of sand and heaps of a mixture of marl and gravel. No nettle colonies were visible in the neighbourhood, but nettle seedlings appeared on the heaps. (Castle Rising and Sandringham).

*In the case of the gravel and marl mixture heaps, the material became solid and cemented together, and the nettle plants grew as detached and bush like individuals with one central rootstock and no developed runners. In the case of the sand heaps, the runners soon ramified the whole heap.

* See also Fig. 141. Section 10.

Patches in fields

From the grazier's point of view, the most important investigation is that into the cause of nettle patches in the fields. There are a large number of causal agencies, all being preventible. In most cases where patches are observed, a careful examination or inquiry will reveal the cause, though it may have been removed or have disappeared.

Molehills, in the same way as rabbit burrows, are a common cause of the introduction of nettles. Molehills often arise on the coarse patches in a field where horses have dunged. The dung attracts insects which in their turn attract moles. When the soil is thrown up in this manner, over a layer of dead grass, an ideal medium for the development of the runners is provided.

In thirty-two instances of nettles occurring in fields it was possible to determine the cause in twenty seven of the cases, either by direct discovery or by inquiry.

The following are examples of causes which have been responsible, where traces were found in the nettle patch, or where persons familiar with the field could remember the cause. Mole hills, felled trees, stick heaps, straw carted from stack yards, abandoned hay cocks, wasted hay, derelict implements, portable hen houses, site where willows were peeled, rabbit burrows, sacking, sludge heaps carted from ditch, dense carpet of dead leaves from willows, drain pipes, dung heaps.

It is possible that in the case of fen soils and light blowing sands, the extremely light condition of the surface soil may in itself provide the necessary open covering layer. Inquiry however has always pointed to the patch having been initiated by one of the causes mentioned in the above paragraph.

Nitrogen Estimations

To determine whether any actual relationship between nitrogen content of the soil and the growth of nettles existed, samples were taken from various sites of nettles on Massingham Heath.

The heath is typical of a poor East Anglian heath, partially overlying sand, and partially chalk. The grass is mainly bent (Agrostis) but large areas are covered by bracken or heather.

Nettle colonies occurred in the following isolated positions on the heath, rabbit burrows, sand heaps, hedges, pine wood, wall of bullock yard at the outskirts of heath.

Samples of soil were taken from each site and from the heath itself as a control.

The sampling was done by means of an auger. Ten borings were taken from each of five rabbit burrow colonies, fifty borings in all. In this case the borings were made through the sand thrown up by the rabbits, and the earth beneath to a depth of eight inches into the latter. The roots were growing in the earth and the overlying sand.

In the case of the sand heaps, hedgerows, and bullock yard wall, the samples were taken in the same manner i.e. fifty borings from each site. In the case of the wood there was a dense carpet of pine needles, and as these were undecayed and no roots were growing in them, the carpet was removed and the borings taken from the actual soil in which the roots grew.

In the sampling of the heath soil, ten borings were taken from about an acre, round each of the five sites.

The following were the figures obtained, the analyses being carried out by Mr.F.Hanley M.A. Advisory Chemist, School of Agriculture, Cambridge.

TABLE XV

No.	Situation.	Loss on Ignition.	*Total Nitrogen
-	-	%	%
1	Massingham Heath	3.46	.106
2	Rabbit Burrows	2.21	.076
3	Sand Heaps	2.12	.062
4	Hedgerows	11.42	.364
5	Walls of Bullock Yd.	7.00	.266
6	Pine Wood.	3.60	.102

Organic matter not passing through an ordinary sieve was found in samples 4 and 6 to the extent of, sample 4: 1.42% sample 6: 0.92%. This was not included in the analysis, but the analyst commented on the large volume occupied by this matter though the weight was small.

In the above results, it will be seen that in three of the five types of sites, the nitrogen content is lower than that of the heath. In cases 4 and 5, the nitrogen content is higher than that of the heath, owing to the excessive amount of organic matter.

The organic matter in case 5, was due to the fact that road sweepings had been thrown against the wall, and not in any way to the bullock yard itself.

Nettles are often associated with organic matter and

* A normal nitrogen content for an old pasture soil would be about 0·25 %. (McConnell.)

as organic matter is associated with nitrogen, the nettle has come to be regarded as a nitrophilous plant. In the writer's opinion, it is the mechanical effect of the organic matter, in providing a light surface covering, which is responsible for the appearance of nettles and not the nitrogen itself. In other words, the "nitrophilous" theory owes its existence to a misinterpreted observation.

In the above connection there are forms of organic matter which have a low nitrogen content, e.g. straw of cereals. Fig 132 shows a recently improvised stackyard in a corner of a pasture field. Undecayed straw has formed a surface covering, and in the space of a few months, nettles have advanced from the hedge and dominated the ground.

Methods of Prevention and Eradication

As the appearance of nettle colonies is due to the presence of a surface covering of the earth, existing in some form or other, it becomes easy to propound preventive measures, i.e. to prevent the occurrence of these surface coverings for any length of time.

Immediate burning or removal of refuse, clean hedge banks, harrowing and rolling of pastures to remove mole hills, in other words clean husbandry, these are the obvious means of obviating the trouble, and are as simple as preventive measures could be. There appears to be an actual reason why nettles should always suggest neglect.

It is not generally realised how quickly nettles will appear and dominate a site, provided conditions are favourable. In the experiment described above with the heap of stones, the stones were built up on July 25th, and within thirteen weeks the nettles were fully established. Many rubbish heaps and piles of litter are left for this length of time before removal, and when a colony is established it is almost impossible to eradicate by grubbing out.

An established colony will provide its own means of advance in the following manner. In the late autumn the plants die and fall forward, the dead stalks and leaves thus forming a surface cover for the advance of the runners in the subsequent season. A colony may thus gradually increase, until a whole field is covered. It is therefore an essential part of prevention to remove dead plants, and after mowing patches of nettles to remove all surface litter to allow the acces of light.

The eradication of nettles may be affected in a simple manner by mechanical means. If a loose surface layer is essential for their existence, conversely a consolidated surface should prohibit their growth. A trial of this method has been carried out by Mr.A.Deptford of Rollingham Hall, Nr.Wisbech, and has proved to be completely successful.

A simple method of consolidation was devised. Where nettles occurred in the pasture, a circular feeding trough or "crib" was placed in the middle of the patch. The cattle trampled round the crib all winter. In the following year the nettles had completely disappeared with the exception of a circular patch which had been covered by the crib.

Unfortunately the inadvertent mowing of this patch prevented a photographic record being made, but an example somewhat similar may be seen in most parks.

Fig.133 shows trees under which cattle do not shelter, owing either to low branches or absence of shade. In this case the nettles grow right to the base of the tree. Fig.134 shows a tree under which cattle do shelter, and it is clearly seen that a zone round the tree is free from nettles. If the cattle are removed the nettles will still fail to penetrate this area.

There appears to be no reason why the consolidation should not be effected by mechanical means. The surface may be cleared and then heavy rolling in wet weather may follow. In mechanical improvement of pasture, it has been found possible to imitate hoof cultivation and consolidation by mechanical means.(20)

When nettles occur at the base of a wall, or in a hedgerow, it is obvious that consolidation cannot be effected, and in these cases only preventive measures are possible to prevent further spread.

Conclusions

Nettles are not a nitrophilous plant in the true sense, their spread is due to a light or open surface covering of the earth.

The runners of nettles are sensitive to exposure. Injury and desiccation cause the death of the runner while exposure to light causes premature developement and consequent weakness of the shoot.

Preventive measures simply involve the immediate removal of all refuse, and other covering material from the land.

Eradication is by mechanical means, and consists of the clearing of the land over the patch, followed by severe consolidation, either by livestock or by suitable implements.

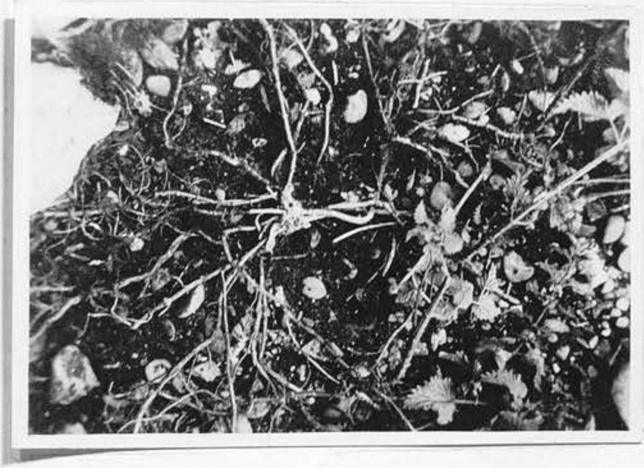

Fig.119. Showing runners of Urtica dioica radiating from central rootstock shingle beach.(Bardsey,Lancashire).

Fig.120. Showing relation of runners to root system in Urtica dioica.

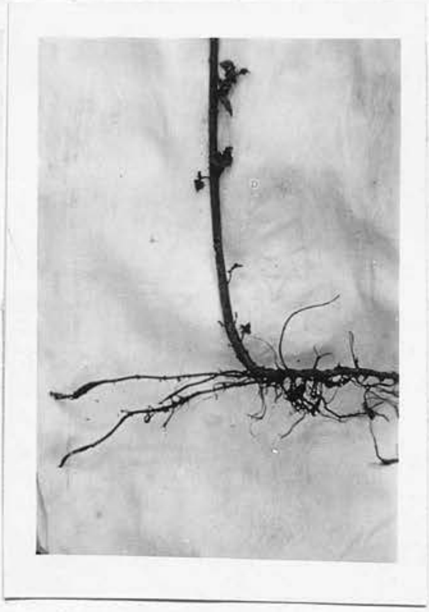

Fig.121. Proliferation of runner in Urtica dioica.

Fig.122. Showing mown grass on hedge bank. A few colonies of Urtica dioica are present in the hedge.(Nr.Sandringham,Norfolk.)

Fig.123. Shoots of Urtica dioica appearing through the mown grass.(fig.122 above).

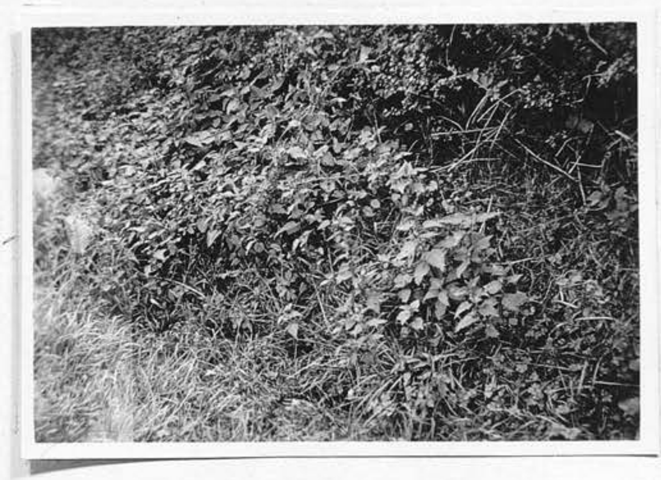

Fig.124. Colony of Urtica dioica established on the bank after removal of the grass.

Fig.125. Urtica dioica appearing through debris on floor of wood (Ryston,Norfolk).

Fig.126. Clearing in wood dominated by Urtica dioica on ground where litter and branches are thickest. Note absence of the species in the foreground and falling off under trees where litter is thin. (Boughton,Norfolk).

Fig.127. Site before building stone heap.(Hawkshead Hill,Lancashire).

Fig.128. Stone heap built on site (fig.127).

Fig.129. Showing Urtica dioica dominating stone heap. (fig.128).

Fig.130. Urtica dioica surrounding rabbit burrows. (Massingham Heath, Norfolk.)

Fig.131.Urtica dioica on sand heaps (Massingham Heath,Norfolk).

Fig.132. Urtica dioica on floor of stack yard. (Babingley,Norfolk).

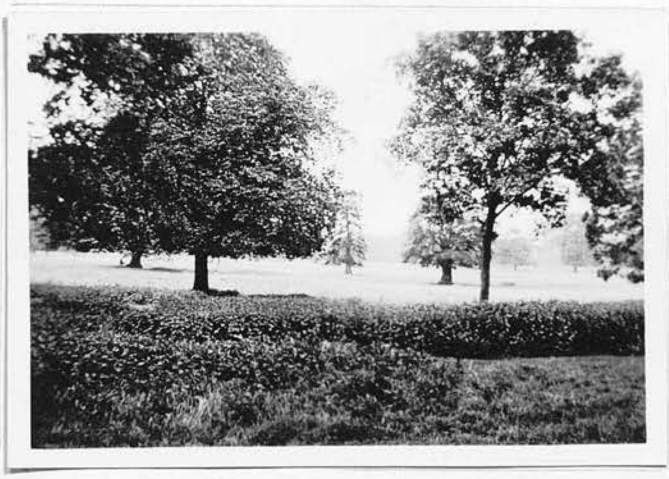

Fig.133. Urtica dioica growing up to base of trees in the absence of treading by cattle.(Ryston, Norfolk.)

Fig.134. Urtica dioica absent on zone where treading by stock occurs.(Ryston,Norfolk).

OVER.

Appendix

Urtica dioica and Nitrifying Capacity of the Soil

It has been attempted by Olsen (33) to show that the distribution of Urtica dioica in certain woods in Denmark is influenced by the nitrate content or nitrifying power of the soil as distinct from the total nitrogen content.

In twelve out of twenty sites the nitrate content and nitrifying power of the soil was higher than in the remaining eight sites. Urtica dioica occurred on ten out of the above twelve sites. On the remaining two sites where nitrate content was high, Urtica dioica was stated to be absent or occurring as a few scattered seedlings. In the remaining eight cases when nitrate content was low, Urtica dioica was absent.

Each site was described by Olsen in detail, and it is a remarkable fact that where Urtica dioica occurred, (i.e. on the sites), surface litter was present, for the site was described as "under oak tree", "near to closely cut beech hedge", "on site of stick heap", etc. In the ten cases where Urtica dioica did not occur there was no surface litter, but a cover of gramineous species was present.

It is obvious that the deposition of surface litter by suppressing gramineous species and providing a surface mulch must increase nitrification in the soil. The writer would contend that the factors of surface litter and higher nitrate content are inseparable. Conversely the development of a grass sward will inhibit nitrification, a fact exploited by fruit growers.

The following investigation was carried out by the writer. Duplicate soil samples were taken from each of three nettle patches, occurring in association with inorganic litter, in addition duplicate control samples were taken from the surrounds of each patch. Onky a scanty vegetation was present on the surrounds.

One sample from each duplicate was treated with toluene in an attempt to check nitrification during transit.

The results together with the analyst's remarks are given below.

The analyses were kindly carried out by Mr. F. Hanley of the School of Agriculture. Cambridge.

	Results on Moist Sample			Results calculated to Oven Dry Ba	
Sample	Moisture %	Total N %	Nitric N Pts/million	Nitric N Pts/million	Total N %
E.C.R. Nettle Patch	17.82	.177	8.3	10.1	.215
" " control	27.21	.230	5.3	7.2	.316
E.C.R. Nettle Patch Toluened	18.68	.168	7.3	8.9	.206
" " control "	26.24	.216	3.2	4.3	.291
E.C.L. Nettle Patch	21.42	.222	7.3	9.3	.282
" " control	26.84	.228	3.2	4.3	.312
" " Nettle Patch Toluened	24.18	.239	9.4	12.4	.315
" " control "	26.78	.199	5.3	7.2	.272
F.C.N. Nettle Patch	23.44	.220	14.7	19.1	.287
" " control	32.91	.284	10.7	15.9	.423
" " Nettle Patch Toluened	24.69	.238	18.9	25.1	.316
" " control "	34.60	.270	9.6	14.7	.413

All percentages by weight.

Remarks. "I would point out that (1.) soil from control patches was always heavier in texture than soil from nettle patches, (2) the soil from nettle patches was drier than soil from control patches, which would favour nitrification at this time of year, (Dec), as such soil would be warmer.

OVER.

Appendix (cont.)

Since the publication of this work it has been suggested to the writer that in favour of the "nitrogen" theory, it may be possible that the deposition of surface material may, by destruction of underlying vegetation, produce a rich store of nitrogen.

It has been further suggested that the nitrogen estimations from sites of nettles, given in this Section, might not have been obtained from samples which were sufficiently localised in the site to demonstrate the above phenomenon. It can only be stated that great care was taken to obtain the samples from soil in which the roots were actually present. The control samples were also taken in a comparable manner.

In the first place it may be stated that Urtica dioica occurs with great frequency on land where the surface cover overlies ground devoid of vegetation. It may also be pointed out that poor sandy arable land, where derelict or badly cultivated, is severely infested with Urtica dioica. It was this phenomenon which lead the writer to doubt the "nitrogen" theory.

Fig: A. illustrates the vigorous growth of the species at the base of a barn wall. This is a common phenomenon, nettles being as frequent in these situations as where nitrogenous material oozes through the wall from the lairages of cattle.

A case came to the writer's notice where a building consisted of a barn and a cow byre. A heap of manure was placed against the wall by the cow house door each winter. On the site of the manure heap the growth of nettles was luxuriant as was that of other species, but the plants were equally abundant all round the whole building and also on some stone heaps at the back of the building (Hawkshead, Lancs).

Fig: B. shows a luxuriant growth of nettles through drain pipes on ground devoid of vegetation. The runners pass through the interstices between the pipes even above ground level.

Lamium album is rarely found not in direct association with Urtica dioica. The former species has exactly the same life form and mode of proliferation as the latter, and when growing apart from Urtica dioica it is always found on sites with some form of surface cover. It may be noted that no claim has ever been made that Lamium album is a nitrophilous species.

The Proliferation of Lamium Album.

An experiment has been carried out with Lamium album, on similar lines to that with Urtica dioica, to test the effect of the removal of the surface cover while the runner is still in the immature state. (Gaywood July - September 1933).

Surface cover was removed from a number of runners while they were only about 6 cms long. The result was the immediate production of a shoot which was thin, stunted and chlorotic. (Fig. C. a.)

The removal of the cover at a more mature stage resulted in a stronger but still badly developed shoot (Fig. C.b.) In both these cases no roots were established at the nodes.

Other runners were left undisturbed and at the time of writing (Sept. 7th 1933) had not developed shoots and had reached a thick fleshy stage and a length of about 25-30 cms. At this stage a constriction forms at the junction with the parent plant the tissues in this region becoming atrophied and losing their succulence. This would appear to sever the connection (as far as flow of sap is concerned) with the parent rootstock. Fig C,c, shows this mature type of runner, the constricted region is visible at the left side of the illustration.

Fig: D. shows the life form of Lamium album.

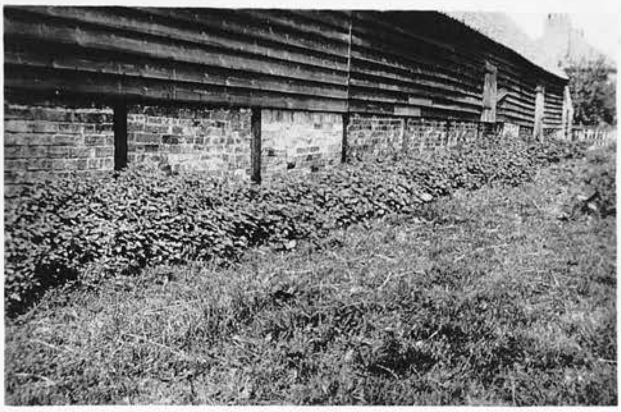

Fig: A. Urtica dioica at base of wall of a barn.
(Black Horse Drove. Isle of Ely).

Fig: B. Urtica dioica dominating site of drain pipes upon a gravelled area devoid of vegetation.
(Hawkshead Hill, N.Lancs.)

d.

b.

c.

Fig: C. Runners of Lamium album A, B, and C. (See text).

Fig: D. Life form of Lamium album (See text).

SECTION

8

THE RELATION OF LEAF SIZE TO ROOT STRUCT

In Trifolium repens

THE RELATION OF LEAF SIZE TO ROOT STRUCTURE IN *Trifolium repens*

Ø The Relation of Leaf Size to Root Structure in Trifolium repens

I. Mechanical Influence upon Root Structure and Leaf Size.

In any observational studies of grassland communities the variation in the leaf size of Trifolium repens, in different situations, is very striking. The relation between this phenomenon and habitat is apparently obvious and is therefore of interest from the ecological point of view. The economic value of T. repens needs no elaboration, this species is the criterion of good pasture in the eyes of the grazier and any factor affecting its productivity or competitive powers demands attention.

It is well known that leaf size is one of the distinctions between ecotypes of this species, but that the characteristic is not purely genetic is explained by the fact that a change of habitat produces a change in leaf size in the same ecotype. If two ecotypes, distinguished by a different leaf size, are removed to a fresh habitat, the increase or decrease in leaf size induced upon them by the new habitat is to a large extent of the same proportion in both cases.

Observation shows very clearly that close cutting or grazing reduces leaf size, this being very noticeable in the case of lawns when the mowing becomes frequent or on sheep walks in the regions of closest grazing. The same result is produced by treading, the effect of which is to remove leaves by damage and thus act in much the same way as cutting or grazing, and in addition to consolidate the soil surface. Fig 15. Sec 3. shows

Ø Accepted for publication. "Journal of Ecology" a colony of Trifolium repens upon a footpath in which the progressive decrease in leaf size towards the region of closest treading is clearly seen.

It is notable also that when runners proliferate from a dense colony of Trifolium repens to an unoccupied area of ground and there establish fresh shoots that the leaves of these shoots are of greater size than those on the centre of the colony. This latter phenomenon may even be observed when a runner establishes a shoot upon a denuded worm cast, in an otherwise dense turf.

It is now a generally accepted fact that the effect of denudation of foliage is to reduce the size and extent of the root system (21). The result is produced by the restriction of photo-synthesis and the consequently reduced food supply to the underground organs. It is obvious that a restricted root range will entail a limited water supply, and it is reasonable to assume that this deficiency may result in an automatic diminution of leaf size as a means of restricting the area of transpiration and consequent loss of moisture. This will explain the phenomena of the observations described above.

Experiments

To investigate the problem of leaf size in relation to root system, a series of four experiments was carried out in the years 1929-30-31-32, the same results being recorded in each instance. The work was carried out in the following manner:-

In each case a garden soil was utilised, in the first two instances a heavy loam (Chesterfield Derbyshire) and in the last two a light loam (Kings Lynn,Norfolk). In both cases the soil was neutral in reaction as the result of frequent liming.

Ten strips of Trifolium repens, each one metre long and containing the same quantity of seed from the same source, were sown each year. The ten strips represented five treatments, each in duplicate, the position of each strip being randomised. It was thought that the above arrangement, and the fact that the trial was conducted four times in four different years would obviate the possibility of soil or seasonal differences.

The treatments chosen were as follows:-

Strips 1 - 1A (Control) strips sown and left undisturbed throughout the season.

Strips 2 - 2A. In this case the seeds were sown in normally loose soil and allowed to become established as seedlings. The soil was then consolidated by treading, care being taken not to injure the seedlings. After consolidation the plants were allowed to grow undisturbed.

Strips 3 - 3A. Trodden and bruised by the foot at weekly intervals commencing two months after sowing.

Strips 4 - 4A. Cut at weekly intervals commencing two months after sowing.

Strips 5 - 5A. These were laid down in the following manner. Containers were constructed from sheets of perforated zinc, each being 1 metre long by 10 cms wide and 10 cms deep. The containers were fitted with handles, filled with soil and embedded in the earth. The seed was sown down the middle line of the container, in the same manner as with the other strips. Eight weeks after sowing the plants were lifted in the containers at weekly intervals and any roots which had emerged through the perforations in the zinc (usually a large crop) were shaved off. The containers were then replaced in the soil. In this manner root range was directly restricted without interference with the foliage.

Results

In each year the following results were obtained:-

Strips 1 - 1A (Control). The growth was luxuriant and the leaves of large size. Had these plants been casually observed in the field they would have been regarded as "commercial" white clover and not as "wild" white clover.

The root system was well developed.

Strips 2 - 2A (Consolidated soil) No difference was noted in comparison with the control as regards leaf size.

The root system was as well developed as in the case of the control, except that there was no growth of secondary roots in the first 2 cms depth of soil. It was also notable that the runners did not establish roots as freely as in the case of the control where the surface soil was loose.

Strips 3 - 3A (Trodden) The results were similar to those obtained by cutting, but the reduction in leaf size was not quite so great. This is accounted for by the fact that treading and partial injury of the leaf does not reduce photo-synthesis so completely as the entire removal of the leaf by cutting. Root range was again restricted, but it was impossible to give any measured comparison with the root range of the cut plants.

Strips 4 - 4A (Cut at intervals). Great reduction of leaf size was shown in comparison with the control. The number of plants did not diminish nor was there any significant difference in the number of leaves.

Root range was definitely restricted.

Strips 5 - 5A (Root pruned only). A great reduction in leaf size was effected, comparable with that noted in the case of the strips which were cut at intervals.

The root range was obviously restricted, but the pruning produced a dense growth of secondaries.

The number of leaves was less than in the case of the cut plants and the difference appeared to be significant.

Observations showed the same results in each year. In 1932, however, it was decided to obtain a definite measure of comparative leaf size. This was carried out in the following manner:-

Leaves were cut in bunches, at the ground level, from each of the strips. The cuts from each strip were placed in separate receptacles and later the produce of each strip was mixed with that of its duplicate. From the five receptacles 100 leaves were picked in succession from each of them, thus giving 100 leaves from each treatment. The leaf area was measured by placing upon graph paper, tracing round the margin, and counting the number of squares covered by each leaf (1 leaf - 3 leaflets). The orthodox method was adopted, i.e. less than half a square was neglected, more than half a squre was counted as one square. (See Table XVI below.)

T A B L E XVI

Strips	Treatments	Average area of leaves	Range of leaf area	Average area expressed as %
1.1A	Undisturbed (Control)	627 sq.m.m.	75-1260 sq.m.m.	100.0%
2.2A	Consolidated Soil	603 " "	68-1184 " "	96.1%
3.3A	Trodden weekly	409 " "	75- 910 " "	65.2%
4.4A	Cut weekly	263 " "	62- 734 " "	41.9%
5.5A	Root pruned	244 " "	60- 750 " "	38.9%

The establishment of shoots from runners made the identification of individual plants difficult, and as estimations would have been inaccurate in consequence they were not carried out. Increase of individuals by runner establishment may have been greater in some cases than in others, but in no case did a treatment reduce the number of individuals.

Discussion of Results

Taking the strips 1 - 1A which were grown in normally loose soil, and left undisturbed throughout growth, as a control or standard, it will be noted that other treatments had a marked effect upon leaf size.

In the case of strips 2 - 2A, the reduction of leaf size cannot be regarded as significant in comparison with the control. The fact that no significant decrease in leaf size can be noted may be explained by the fact that treading produces consolidation in the first 2 - 3 cms of soil only, below this level the density of the earth is comparable with that which is unconsolidated. The clover plant is able to force its strong tap root through this surface layer and to spread its deep root system through the lower soil. It appears that the only effect of this surface consolidation is the restriction of the developement of secondary roots in the region of this layer and the difficulty in establishing adventitious roots from runners, owing to the hardness of the soil surface. The root system as a whole was almost as well developed as in the control.

In the case of other species such as grasses or other shallow rooting plants, this consolidation of the top layer of soil may restrict root range and leaf size. It has been shown that where the soil has been consolidated to a depth by packing in layers (see page 52) that the whole of the plant of the several species grown was restricted in growth.

Strips 3 - 3A showed the same result from treading the leaf as from cutting, though the restriction in size was not so great. This latter comparison is probably explained by the fact that crushing by the foot does not effect so complete an obliteration of leaves as does the cutting, though this depends on the intensity of the treading.

In the case of strips 4 - 4A the effect of cutting had a very rapid effect on leaf size; after the first cutting the second crop of leaves was smaller, and there was a steady but diminishing reduction after each subsequent cutting. Root range was restricted in developement to a greater extent than in any other treatment.

The fact that in the case of strips 5 - 5A where the plants were root pruned only there was a great reduction in leaf size, comparable with that produced by cutting at weekly intervals, is of great significance.

This result points to the fact that reduction in leaf size is not directly due to cutting or crushing of the leaf, but to the consequent effect on root range and water supply which in its turn automatically reduces leaf size.

In the case of the root pruned strips the root is directly restricted without interference with foliage, but it is obviously impossible to reverse the process, i.e. to cut or crush the foliage without restricting root range. It can therefore never be more than an assumption that cutting or crushing has no direct influence on leaf size. The effect of root pruning does definitely prove that root restriction can be fully responsible for diminution of leaf size, apart from any direct mechanical influence upon the leaf. As leaf size is reduced by root prunning to as great an extent as by cutting or crushing, it does point to the fact that these latter processes do not reduce leaf size by any direct means.

It is worth noting that the different sizes of leaf on any clover plant, arbitrarily placed in two groups, large and small, exhibit a distinct stratification, i.e. an upper stratum of large leaves and a lower one of small leaves. It would be reasonable to assume that the influence of cutting or treading in reducing leaf size simply constitutes the removal of the upper layer, but this is disproved by the fact that root pruning also inhibits the formation of this upper stratum of large leaves.

II Soil Acidity and its Influence upon Root structure and Leaf Size

Influence of Soil Acidity on Root Structure

It has been known for some time that Trifolium repens tolerates a high degree of soil acidity (22). Observations upon very acid soils in the Midlands and North of England showed that plants growing upon these soils possessed a comparatively smaller leaf than upon a neutral or alkaline soil, but there were a few puzzling exceptions. On examining root structures it was noted that in some cases the whole root system was restricted in size, while in others it appeared to be fairly well developed in certain layers of the soil, in other words to exhibit stratification.

* On many soils there is a definite stratification of soil acidity due largely to biotic influences. Acidity may be more intense in the surface layers of the soil owing to the formation of acids in the surface layer of dead root material or "mat", and the CO_2 from living roots. In industrial districts acid fumes may be the cause of this surface acidity, and may also assist indirectly in the formation of "mat".

Sometimes the acid surface layer is ploughed completely under, thus forming an acid stratum at a depth in the soil. Acid pans may also produce this effect.

In cases where liming has been carried out the surface layer of an acid soil may become alkaline or neutral in reaction, in consequence of the liming.

A soil may also be acid throughout.

On examining root systems in the field, and at the same time making field tests of the intensity of acidity of the different layers of soil by means of soil indicator; (approximate P_H value determined by B.D.H. Universal Indicator) it was noted that the root system definitely reacted to the acidity of the soil at different depths. Root developement was restricted in the most acid layers and comparatively better developed in the alkaline, neutral, or less acid layers of the soil. There was also a definite inhibition of nodule formation in the most acid layers.

* Worm casts may produce a neutral surface stratum. (See Section 9). In stable soils there may be a decrease in acidity, as depth increases, due to leaching of carbonates.

Experiments

The stratification of soil acidity was never sharply defined in the field and no strict line of demarcation could be drawn. In many cases the difference in the P_H value of one layer did not exhibit a wide range of difference with that in another. For this reason one could not take any measure (photographically or otherwise) of the corresponding stratification of the root system, but observation left no doubt as to its existence.

To confirm the above observations and produce definite illustrations, a series of experiments were set up as follows:-

In the year 1928 plants of Trifolium repens were grown in a garden soil of neutral reaction (P_H 7 approx) into which layers of very acid soil (P_H 3 approx) were introduced. The acid soil was, as far as possible, of the same physical texture as the neutral. Both soils overlay coal measures shale, but the neutral soil owed its condition to frequent and heavy liming. The experiment was not carried out in pots as this leads to a felt like formation of root fibres against the surface of the pot. Garden borders were utilised.

When the plants had flowered and the seed formed, their root systems were examined by the following method:-

The plants were excavated with the block of soil in which the roots were growing, preserved intact. The block was wrapped with fine mesh netting and pierced with wire skewers to keep the roots in place. After the soil had dried it was shaken gently until all the particles fell away from the roots, any lumps adhering to the roots were crushed with the fingers. (The system of washing out the roots, adopted by some workers in the U.S.A. and Russia, was found impracticable as it resulted in a felting together of the secondary roots).

Results showed clearly the reaction of the secondary roots to the stratification of acidity.ØØ

In the following year a similar experiment was carried out with the same results. The effect on the root systems of plants of Trifolium pratensis was also observed and the same reaction was noted.

A further trial was carried out in 1931 on a sandy soil (P_H 6.approx) with a lime content of 0.40% $CaCO_3$. Layers of sandy acid soil (PH 3.approx) lime requirement 0.063% CaO were introduced. In this trial dense patches of Trifolium repens were grown by heavy seeding. Figs.135,136, and 137, show the same results as in the 1928 experiment

Influence of Soil Acidity on Leaf Size

Observations in the field showed that where a neutral surface layer overlay an acid soil, the germination and establishment of Trifolium repens and other cultivated plants was vigorous. It is now a generally accepted fact that a thin layer of neutral or alkaline soil is sufficient to stimulate germination and establishment on an acid soil, in the case of several grasses (23). In the case of the

ØØ The photographs to be published in "Journal of Ecology."

establishment of Trifolium repens under these conditions the plants in the early stages were vigourous as compared with those grown on an all acid soil. This was demonstrated experimentally in pots, and is often observed in practice. It was noted, however, both in the field and in the pot experiments, that when a drought ensued, the plants wilted. The larger leaves died off and a smaller leaved plant resulted, comparable with that grown in an all acid soil. *On an examination being made it was found that the root system had developed in the neutral surface layer, at the apparent expense of root range.

When an acid layer occurred at a certain depth, the leaf size did not appear to be affected. The root range as a whole suffered no restriction.

Experiments were set up in 1932 to confirm these observations, and to obtain definite data with regard to leaf size.

Plants were grown in (1) Acid soil with a neutral surface layer. (2) Neutral soil with acid surface layer. (3) All acid soil. (4) All neutral soil, (Strips 1 - 1A of the previous section of this work were taken as the example of an "all neutral soil." This was the neutral soil used in (1) & (2) in this paragraph.

The following were the differences in leaf size, the estimation being made in the manner previously described:-

* A similar condition is described in acidophilous plants, growing in an acid surface layer, overlying calcareous soil (J. Braun-Blanquet. "Pflanzensoziologie")

T A B L E XVII

Example.	Soil.	Average size of leaves.	Range of leaf area	Average area expressed as %
1.	Acid soil Neutral surface.	320 sq.m.m.	65-763sq.m.m.	51.0%
2.	Neutral soil acid surface	369 " "	58-983 " "	58.8%
3.	All acid soil	280 " "	61-808 " "	44.6%
4.	All neutral soil	627 " "	75-1260 " "	100.0%

In example 1 leaf size was reduced in comparison with example 4. In example 2 some relative reduction was noted, but in example 3, the leaf size was as reduced as in example 1. Example 2 was checked in growth in the early stages owing to germination having taken place in an acid medium.

Summary

It is shown that restriction of leaf size may be produced by the mechanical operation of cutting or crushing the leaf. These operations interfere with the nutrition of the root system, thus reducing root range. A restricted root range results in a limited water supply which automatically produces a smaller leaf, and consequently a smaller area of transpiration. Direct root pruning produces the same phenomena.

Soil acidity may occur throughout the whole of the soil, or in strata. Stratification of soil acidity produces stratification of root developement, the secondary roots being undeveloped in the acid strata.

When soil acidity restricts root developement, leaf size is also reduced in proportion to the degree of restriction.

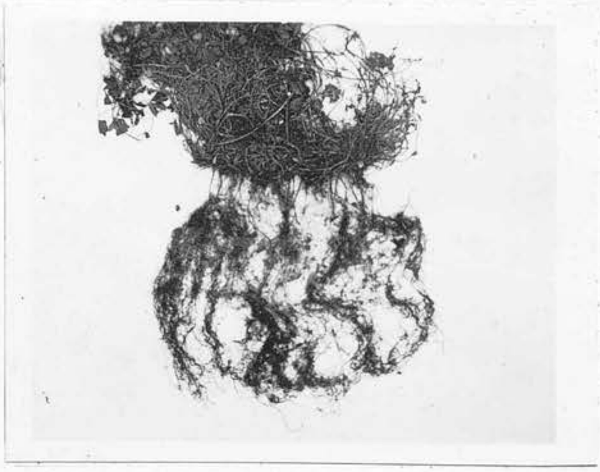

Fig.135. Showing stratification of root system in relation to stratification of soil acidity. Note absence of developement of secondary roots in acid layer.

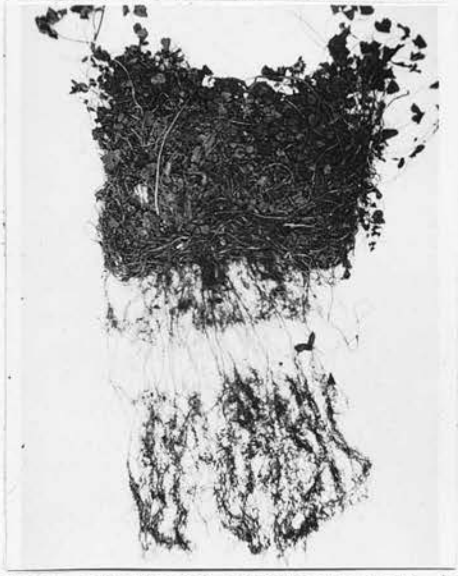

Fig.136. Showing similar phenomenon to Fig.135 above.

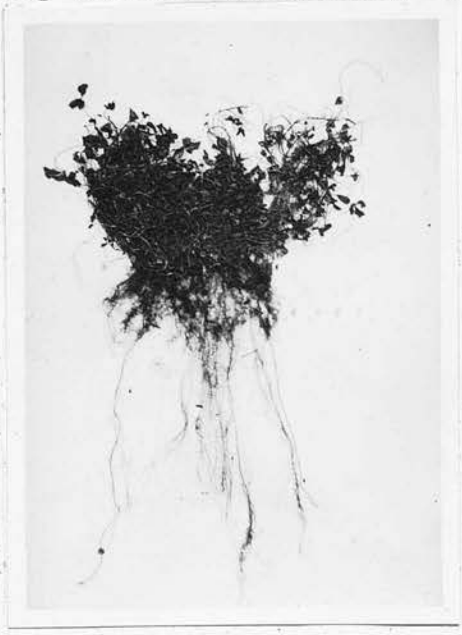

Fig.137. Showing similar phenomenon to Fig.135 & 136 above.

SECTION

9

THE DISTRIBUTION OF WILD WHITE CLOVER

(*Trifolium repens*)

IN RELATION TO THE ACTIVITY OF EARTHWORMS

THE DISTRIBUTION OF WILD WHITE CLOVER (*Trifolium repens*) IN RELATION TO THE ACTIVITY OF EARTHWORMS (*Lumbricidae*)

THE DISTRIBUTION OF WILD WHITE CLOVER (Trifolium repens) IN RELATION TO THE ACTIVITY OF EARTHWORMS (Lumbricidae)

A connection between the presence and abundance of Trifolium repens and the activity of Lumbricidae has long been recognised. This is most obvious to any observer, but apart from expressions of opinion of a varying nature, no definite investigation of the problem appears to have been carried out.

Graziers have recognised the activity of earthworms as evidenced by the abundance of "casts" as an indication of good pasture or as evidence that improvement is taking place. Greenkeepers and those concerned with the care of lawns recognise the relationship described above, but in this case the occurrence is undesirable.

In work on the mechanical improvement of pasture an attempt has been made to stimulate the propagation of Trifolium repens by the use of a roller with curved spikes, the action of which is to throw up little mounds of earth resembling worm casts. This operation has not met with any degree of success (24).

Opinion has been expressed that Trifolium repens is stimulated in developement by the fine mulch of bare earth provided by the casts, by the chemical nature of the casts, or on the other hand by the possible attraction of Trifolium repens as a source of food for Lumbricidae. Preliminary investigations soon disclosed a more complicated and indirect relationship.

Distribution of Trifolium repens in Relation to Number of Casts.

An attempt was made to determine whether the number of worm casts present on a soil surface was a measure of the population of Lumbricidae in the soil. It appeared that

Accepted for publication "Welsh Journal of Agriculture." 1933.

a correlation did exist as was to be expected, but difficulty in excavation and the sorting out of the worms from the soil made accurate measurement impossible, further it was not possible to estimate to what depth the worms may be found.

The absence of data with regard to the above correlation does not materially affect this enquiry as it is the number and total weight of casts which is of importance rather than the number of organisms which produce them.

Activity, as manifested by casts, varies seasonally and periodically due to the physical condition of the soil with regard to moisture and temperature. At any given time, however, the difference in the number of casts on a given area of soil surface on a certain tract of land, and the number of casts on another area of the same dimensions on the same tract of land is a reliable measure of the comparative activity of Lumbricidae on those areas.

To obtain data with regard to the apparent relationship between Trifolium repens and worm activity, as manifested by casts, a survey was carried out on certain types of land in the County of Norfolk. The following method of survey was adopted.

In January 1932 during mild weather, three areas were chosen. Massingham Heath, overlying sand or chalk. Wooton Sand Pits, on sandy heath. Riverside Gaywood, alluvial soil. All sites were situated in the County of Norfolk.

The method of taking counts, adopted in all cases, was to traverse the ground in various directions making random throws with a metre quadrat. Readings were taken to ascertain the percentage area of the ground, within each quadrat, covered by Trifolium repens. At the same time the number of worm casts in the quadrat were counted.

The quadrats were arranged in groups a,b,etc., (See Table XVIII column 1) according to the type of vegetation which characterised them. Those quadrats which contained any proportion of Trifolium repens were placed in separate group (e.g.Group d Table XVIII) and subjected to more detailed analysis (e.g.Table XIX). In the case of the latter groups containing Trifolium repens the casts were collected from each quadrat and weighed, the total weight of casts on each quadrat being recorded.

It was difficult in some cases to distinguish true worm cast from earth adhering at the base and for this reason only the definitely shaped part of the cast was collected. In Group b Table XXII it was impossible to obtain accurate weighings of the worm casts and for this reason no further examination was made of this group. Inaccurate weighing was due to the wet condition of the ground and the close grouping of the casts.

The results obtained are set out in the following tables.

TABLE XVIII

Massingham Heath (200 Counts)

1. Group	2. No.of Quadrats per group.	3. Vegetation Type	4. % area of T repens	5. Casts per Quadrat.	6. Av.No. of Casts.	7. Total of Casts
a	153	Erica. spp, Pteris, Agrostis, Festuca,	0	0	-	0
b	19	"	0	1-2	1.42	27
c	21	"	Trace	1-4	2.80	59
d	7	Festuca, Agrostis, Lolium, Poa and T.repens	2½%-8%	10-36	26.00	182

TABLE XIX

(Detailed examination of Group d Table XVIII above).

1 Quadrat	2 Vegetation other than Trepens.	3 % Area covered by T: repens.	4 No. of Casts.	5 Total weight (air dry) of Casts.	6 Av weight (air dry) of Casts.
1	Agrostis-Festuca	2.5	17	60.0 Gms	3.50 Gms.
2	" "	4.0	10	27.0 "	2.70 "
3	" "	5.0	36	135.0 "	3.72 "
4	" "	5.5	27	84.0 "	4.20 "
5	Agrostis Lolium Poa	5.5	31	120.0 "	3.87 "
6	" " "	6.0	29	108.0 "	3.72 "
7	" " "	8.0	32	105.0 "	3.27 "

TABLE XX

Wooton Sand Pits. 100 Quadrats.

1 Group	2 No. of Quadrats per Group.	3 Vegetation Type	4 % Area of T: repens.	5 Casts per Quadrat	6 Av: No of Casts.	7 Total Casts.
a	33	Bare Sand	0	0	0	0
b	59	Erica spp Pteris	0	0	0	0
c	2	ϴ Blown Sand	Trace	5-17	11.00	22.00
d	6	Agrostis Lolium Poa & T: repens	3-30	20-72	32.33	193.98

ϴ Remains of dead vegetation found at a depth of about 10 cms.

TABLE XXI

(Detailed examination of Group d Table XX above).

1 Quadrat	2 Vegetation other than Trepens.	3 % Area covered by T: repens	4 No. of Casts	5 Total Weight (air dry) of Casts.	6 Av. weight (air dry) of casts.
1	Agrostis, Lolium Poa	3.0	20	135 Gms	6.75
2	" " "	5.5	27	126 "	4.66
3	" " "	6.0	24	93 "	3.87
4	" " "	8.0	31	165 "	5.32
5	" " "	10.0	20	108 "	5.40
6	" " "	33.0	72	300 "	4.16

TABLE XXII

Riverside Pasture Gaywood. (20 Quadrats).

1	2	3	4	5	6	7
Group.	No. of Quadrats per Group.	Vegetation Type	% Area of T: repens.	Casts per Quadrat	Av: No of Casts.	Total Casts.
a	7	Coarse patches, Dactylis Agrostis & Holcus.	Trace	4-11	5.57	39
b	13	Lolium, Poa, T: repens.	10-30	30-87	77.61	1009

Owing to the wet condition of the ground and the large number of casts occurring in groups, the figures in the above Table XXII, Group b, columns 5, 6 and 7 are only approximate. Owing to the difficulty in separating the casts from the soil with precision no weighings were taken. For these reasons no detailed tabulated examination of Group b can be made.

Tables, XVIII, XX and XXII above show clearly that areas which exhibit worm casts coincide exactly with those containing in their vegetation a proportion of T.repens.

There appears from an examination of Tables XIXand XXI columns 3, 4 and 5 to be a certain correlation between the abundance of worm casts on a given area and the proportion of the ground covered by T.repens.

The Nature of Worm Casts.

Before preceding further with the investigations it was considered necessary to examine the nature of worm casts in comparison with the underlying soil.

Casts may be divided into two types, i.e. the type formed from the top soil and vegetable matter drawn in from the surface and the type produced when the earthworms are working in the sub-soil. When the latter part of the earth is of lighter colour than the top soil the casts from this region may easily be distinguished by eye. Observation shows that taking the year throughout "subsoil casts" are comparatively insignificant in number. Their abundance varies periodically.

In the year 1929 two samples of worm casts were collected, (one from Sutton Park, Derbyshire on acid soil overlying Coal Measures shale, and one from the side of a macadam limestone road). Soil samples were collected from the underlying soil in each case, in the approved manner.

The samples were submitted for a "Lime requirement" test (a measure of soil acidity) with the following results, Table XXIII below.

TABLE XXIII.

(100 casts per sample).

Sample.	Description.	Lime Requirement % CaO
1	Worm Casts - Sutton Park.	Nil.
1a	Adjoining Soil " "	0.115
2	Worm Casts - Macadam Road.	Nil
2a	Adjoining Soil " "	Nil

A further sample was collected from Hardwick Park, Derbyshire. In this case the top soil overlay a light coloured and sandy subsoil, and the worm casts were definitely of the subsoil type.

The results are set out in Table XXIV below. Compare with casts in Table XXV which are of the "topsoil" type.

TABLE XXIV

(100 casts per sample)

Sample.	Description.	Lime requirement % CaO	Exchangeable CaO	Nitrogen.
1	Worm Casts	0.070	0.632	0.410
1a	Adjacent Soil	0.149	0.632	0.480

The above analyses were carried out by Mr.H.T.Cranfield, Advisory Chemist of the Midland Agricultural and Dairy College.

A further series of samples were taken in the County of Norfolk in the year 1931. The analyses were made by Mr.F.Hanley Advisory Chemist of the School of Agriculture, Cambridge,(who carried out all subsequent analyses)

* The following results were obtained.

TABLE XXV (100 Casts per Sample)

Sample	Description	Presence of $CaCO_3$	Exchange-able CaO%	Lime Re-quire-ment %CaO	Total Nitrogen
1 Casts	Massingham Heath. Chalk	0.32%	0.328	Nil	0.368
1a Soil	" "	Nil	0.113	0.104	0.224
2 Casts	Gaywood.Garden Soil	0.65%	0.360	$CaCO_3$ present)	)0.395
2a Soil	" " "	0.40%	0.320	"	)0.318
3 Casts	Wooton Sand Pits.	4.70%	0.259	$CaCO_3$ present)	)0.220
3a Soil	" "	0.65%	0.123	"	)0.111
4 Casts	Massingham Heath.Sand	Nil	0.300	0.035	0.325
4a Soil	" " "	"	0.122	0.063	0.167
5 Casts	" " "	- ø	0.484	Nil	0.430
5a Soil	" " "	- ø	0.368	Nil	0.193

ø Figures not determined.

It is seen from the above table that where $CaCO_3$ is present in the soil there is a still higher percentage present in the casts. In example 1 & 1a $CaCO_3$ is absent in the soil there being an acid condition with a lime requirement of 0.104% CaO,but in the casts $CaCO_3$ is present to the extent of 0.32%. In cases, e.g.example 4 & 4a,where both soil and worm casts are acid, there is a lower lime requirement in the casts than in the soil.

* Similar results have been obtained by D'Auchald, and by Salisbury, though no distinction was made between "subsoil" and "topsoil" casts. (34) (35.)

In all cases in Table XXV the exchangeable calcium is higher in the casts than in the soil. It is also notable in all examples in the above table that there is a higher percentage of nitrogen in the casts than in the soil, this may be taken as expressing a higher content of organic matter. In the case of a subsoil type of cast (Table XXIv) the organic matter content is lower than that of the soil and consequently there is a lower percentage of nitrogen in the cast than in the soil.

The higher nitrogen or organic matter content of the cast as compared with that of the soil is easily explained by the well known habit of Lumbricidae in drawing in vegetable matter from the soil surface. During excavation at a lower level, as evidenced by a "subsoil cast", there is no ingestion of vegetable matter, and this is shown in the analysis of the cast.

The problem of the higher calcium carbonate content (or lower acidity) of the cast as compared with the soil is a somewhat complex one. Three explanations might be offered:-

(a) The presence of calciferous glands in Lumbricidae, these excrete or secrete calcium carbonate into the alimentary canal. Several theories exist as to their proper function (25

(b) The subsoil may contain a higher calcium carbonate content than the topsoil or may be of a lower degree of acidity. This may be exploited by Lumbricidae.

(c) The ingestion of organic or vegetable matter, from the soil surface, possessing a higher proportion of calcium compounds than the soil.

The existence of calciferous glands which may excrete calcium carbonate spasmodically, might explain the higher calcium carbonate content of some casts than of others on the same site. It does not explain the fact that all casts contain more calcium carbonate or are of a lower degree of acidity than the soil, for if the glands are responsible for this condition of the casts they must be supplied by calcium from some source other than the soil. That the casts contain a higher <u>total calcium</u> content than the soil was shewn by the following investigation.

A sample of casts (about 200) was collected from a site on Massingham Heath, the soil was also sampled in the approved manner.

The result of analysis was as follows:-

Casts	0.134% Total CaO.
Top 12" of Soil	0.077% " "

As regards the subsoil being exploited as a source of calcium this appears to be a possibility upon first consideration. An investigation showed that in a certain case where the soil and the worm casts both showed a lime requirement the soil possessed a higher requirement than the casts, but below a depth of 1 ft the lime requirement diminished.

In this case casts were collected over an area of about 500 square yards. (Massingham Heath, Norfolk).

The soil was then sampled throughout each foot depth to a depth of 7 ft. This sampling was facilitated by the fact that the area was being excavated for sand. The results are set forth below in Table XXVI.

TABLE XXVI.

Sample.	Lime Requirement as % CaO.
Casts.	0.120
1 Ft. Depth	0.154
2 " "	0.092
3 " "	0.067
4 " "	0.107 (Acid pan)
5 " "	0.044
6 " "	0.053
7 " "	0.044

It would appear that the less acid soil of the casts might be obtained from the subsoil. The casts were however definitely of the top soil type, being of the same colour as the soil. The latter which was 10" - 12" deep was of a greyish black colour, while the subsoil was a golden yellow sand, there was a sharp line of demarcation between the two. Further it was revealed upon analysis that the respective nitrogen contents were as follows :-

"Casts" 0.258 % Nitrogen.
Soil (to12")0.125 % "

It is obvious that if Lumbricidae were exploiting the subsoil the organic matter and nitrogen content of the casts would be lower than that of the soil. As in all cases (except Table XXIV where "subsoil casts" are represented) the nitrogen content of the casts is higher than that of the soil, it is reasonable to assume that topsoil casts are composed to a certain degree of vegetable matter drawn from the surface of the soil. It is therefore reasonable to assume that this material is the source of the calcium which goes to raise the proportion in the cast above that in the soil. Darwin suggests that the calcifercus glands may function to eliminate calcium obtained from dead vegetation which earthworms devour (26).

It is seen that worm casts are of two types e.g. "Topsoil" and "Subsoil". The relative abundance of the latter appears to show seasonal variation probably coinciding with periods when excavation is taking place, due to changes in temperature. All casts appear to show a higher calcium carbonate content or lower degree of acidity than the soil. In the case of a "subsoil cast" there is a lower nitrogen content than that of the soil, but in a "topsoil cast" the nitrogen content is higher than that of the soil.

As "subsoil casts" are greatly in the minority, it may be stated that an accumulation of worm casts on the soil surface provides a superficial layer of soil of higher calcium carbonate content or lower acidity, and of higher nitrogen and organic matter content than the rest of the soil as a whole.

The rate of accumulation of casts varies in direct proportion to the activity of Lumbricidae, but there is every reason to believe that the figure given by Darwin i.e. 0.2" per annum is a fair average (27).

<u>The Relationship between T.repens and Lumbricidae.</u>

In examining any possible factors influencing the connection between the two organisms it is worthy of note that while T.repens is not found in nature in the absence of Lumbricidae, as evidenced by casts, Lumbricidae are often found in the absence of T.repens, e.g. in gateways and upon earth from which vegetation is removed. If one organism were dependent upon another it would appear that T.repens is dependent upon Lumbricidae rather than the reverse.

Calcium-carbonate Content of Soil. This appears to bear some relationship to the problem for it has been observed that casts are scarce on acid patches in a field and comparatively abundant in neutral areas (28).

It has been suggested in this connection that calcium carbonate in the soil is essential for the calciferous glands, but this may not be the case for it is not certain that the glands are not merely excretory (25) (26). If calcium is essential it is not necessary for it to be in the form of a carbonate in the soil, but it may be obtained, as already shown, from the covering vegetation.

It must be borne in mind that acidity or neutrality of the soil may affect Lumbricidae markedly, but still indirectly, for it is well known that neutral patches are closely grazed while the adjoining acid patches are overgrown and matted.

The activity of Lumbricidae may in itself do much to reduce acidity, aeration by burrowing will hasten humus decomposition, and the casts will produce a neutral or less acid surface layer of earth.

Worm casts and T.repens rapidly appear on an acid soil where the overgrown herbage is mown closely and frequently to produce a lawn or putting green without laying fresh turf.

It is described later in this work how when turf was removed from a heath soil, it was seen that the number of casts on the exposed areas increased from 8.8 per sq metre before removal of the turf to 22.7 per sq metre 12 weeks after removal of the turf. In this case the soil was in an acid condition (P_H 5 approx with estimated lime requirement of 0.063 % CaO).

It is now known that Trifolium repens will tolerate intense acidity (22). This species will in the absence of competition grow abundantly on acid soil.

Lumbricidae and the Establishment of Trifolium repens.

In the first place, the surface covering of casts may be a factor of some significance. An experiment by the writer showed that Trifolium repens germinated better in a medium of casts than in one of the underlying soil. In a surface layer of casts, however, a superficial root system was developed and the plants suffered in consequence during drought. (See also Sec 8. page, 148.)

It has been clearly shown in the above connection that other species such as Agrostis benefit by a superficial neutral medium for germination (23). There appears no reason why casts should stimulate germination and growth of Trifolium repens more than the other species which compete against it.

The deep burrowing of Lumbricidae cannot be of greater benefit to Trifolium repens than any other species for though this may encourage drainage Trifolium repens may tolerate a certain degree of water-logging of the soil.

It has been shown that illuminated areas, when overshadowing influences are removed, exert a great attraction upon Trifolium repens (See, Section 3. page. 58.)

It may be noted upon observation that when a cast occurs in a dense turf and causes a small bare patch of soil that the runners of Trifolium repens are attracted to this area, and upon it develope larger leaves than on the surrounding sward.

The above phenomenon may be of some significance, but cannot be of primary importance for if this were the case the appearance of worm casts on a newly made lawn or green would precede the development of Trifolium repens, but the two phenomena appear to materialise at the same rate. It was further noted that where large numbers of small heaps of earth resembling worm casts were produced artifically, by a machine, an experiment carried out at Hardwick Park Derbyshire (24), no significant increase in the developement of Trifolium repens was produced.

Trifolium repens as a Food for Lumbricidae. The possibility of Trifolium repens attracting Lumbricidae as a food must be considered. In a large number of cases where Trifolium repens and other species were grown in pure culture, it was found that there was no greater number of casts per sq metre upon the clover plots than upon the bare earth, though it ws noted that casts were less abundant upon plots of Agrostis or Festuca ovina where a thin mat of surface root had formed. The above observations were made upon demonstration plots of Trifolium repens and gramineous species grown for educational purposes in pure culture. (Chesterfield Derbyshire, & fields plots Oxburgh, Norfolk).

The Influence of Bare Ground

In studying the distribution of Lumbricidae, as evidenced by casts, it becomes very apparent that this organism prefers areas where the turf is open, and also bare areas of ground. Observations were made upon a dense turf of Agrostis and Festuca (Massingham Heath, Norfolk). Careful examination failed to reveal more than an average of 8.8. casts per sq metre. On the same site areas of varying dimensions were exposed, by the turf being removed for lawn making. * Upon this bare earth casts began to appear in increasing numbers until up to the end of twelve weeks when the number of casts had increased to an average number of 22.7 per sq metre.

While the number of casts were increasing it was noted that isolated plants of Trifolium repens appeared, apparently from remains of previous rootstocks, these plants spread rapidly upon the bare surface. A few annual species also appeared. A fringe of Trifolium repens began to form around the margin of the bare areas, this fringe was formed by runners from plants existing in the turf and attracted to the light.

All observations demonstrate clearly that areas rendered devoid of vegetation, owing to some biotic influence, and not owing to infertility, or areas where close cutting or grazing of the herbage occurs, each prove an attraction to both Trifolium repens and Lumbricidae.

<u>The Influencing Factors</u> The stimulus to Trifolium repens is that of illumination as this species is greatly influenced by this factor. As soon as bare earth is exposed or overshading herbage removed, the species is attracted towards the illuminated area.

* The increase was not a seasonal one as subsequent observations upon similar situations (and upon their surrounds as a control) have confirmed the phenomenon

In the case of Lumbricidae, the influencing factor appears to be increased water supply. *Surface ventilation may be of some consequence, but the attraction of increaased moisture becomes obvious during any survey. Lumbricidae are very sensitive to drought and, upon dry conditions prevailing, will aestivate in a specially constructed chamber, being found coiled into a ball in this cell of earth. This dependence upon moisture is widely known. (36.)

It may be observed on any garden path, when a drought breaks and the earth becomes moist again, that worm casts first appear in the depressions where moisture collects. This may also be demonstrated by watering a small area. In fields where the land is laid in ridge and furrow, activity commences in the furrow at the breaking of a drought. This latter phenomenon is not only evidenced by the appearance of worm casts, but also by the appearance of molehills which indicate the presence of Lumbricidae.

When areas are exposed by the removal of a turf it will always be found that the exposed soil is moister than that underlying the turf (See Sec.11 p.185) The vegetation and the mat of root material prevent free access of moisture, and in addition there is greater loss of moisture by transpiration from the foliage on the undisturbed areas, this always provided that the bare soil is not cultivated by digging or fallowing and loss of moisture induced in this way. Close mowing reduces loss by transpiration and inhibits root development thus producing the same conditions as by removing the turf, though to a lesser degree.

* Earthworms are sensitive to an excess of CO_2 in the soil atmosphere ("The Oligochaetae". Stephenson. Review of research)(36) The air of soil underlying grass may contain 1.6% CO_2 as compared with 0.2.% CO_2 in arable land soil. (Figures taken from Rothamsted soil. Russell and Appleyard 1915)(37): Leather obtained evidence that CO_2 is higher near plant roots. (38)

Conclusions.

The association of T.repens with the activity of Lumbricidae appears to be an indirect one, in that conditions produced by the biotic factor, i.e. the exposure of bare earth or the defoliation of herbage, produces conditions favourable to both organisms.

In the case of T.repens the attraction is increased illumination, in the case of Lumbricidae it is increased moisture, and soil ventilation.

A layer of worm casts by virtue of its chemical and physical composition produces a surface mulch which wil conserve soil moisture and provide a medium stimulating the germination and establishment of seedlings, but this does not specially favour the propagation of T.repens in proportion to other species.

SECTION

10

THE MECHANICAL INFLUENCE OF THE BIOTIC FACTOR

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The object of this section is to consider as a separate entity the mechanical influence of the biotic factor as expounded in the main part of this work. In addition to this review, a detailed examination is made of mechanical influences of domestic and other animals.

A complete understanding of mechanical influences upon vegetation, and the relative importance of each type of influence, is of value from several aspects. In the first place it may do much to explain the past history of any piece of ground which is covered by vegetation. Secondly it may provide the key to some of the problems of the animal ecologist, and thirdly the knowledge may be exploited economically as will be shown in Section 11 of this work.

Human and Animal Influences

Treading

Probably the greatest influence exerted by humans upon vegetation is through the agency of treading, this is also shared by domestic animals.

The mechanism of treading is a peculiar one, and is not to be compared with that of ordinary consolidation by rolling, or with the defoliating effect of mechanical mowers. A close observation of the action of the foot either of humans or of animals shews that there are two distinct movements, a vertical and a horizontal one. In the first place the foot is brought down to the ground and raised again, this produces a purely compressing action resulting in a slight amount of injury to gramineous species and a definitely fatal effect upon tall herbaceous species. This action is however only comparable with that of mechanical compression in the form of rolling.

The second movement in treading, i.e. the horizontal one (the twist of the foot or hoof occasioned by forward movement) is the one which distinguishes treading from simple compression. This action produces a serious bruising effect upon the species such as would not result from pressure only. In addition there is a certain amount of suction produced which brings soil to the surface in wet weather.

It has been shown that the action of treading is fatal to certain species while others by virtue of their life form are enabled to effect a recovery. These latter species are Poa pratensis, Lolium perenne, Dactylis glomerata, Cynosurus cristatus and also Trifolium repens and Plantago spp.

There are some species which exhibit a greater resistance and power of recovery than others, while treading may be so severe as to destroy all species. It will be seen that not only does treading produce a synusia of species, but also a zonation of the species composing the synusia in response to the varying degrees of treading.

Treading produces a consolidated or crusted condition of the surface layers of soil. This appears to produce a prostrate rosette habit in many species. It also causes root restriction, and consequent reduction in leaf size.

An indirect influence of treading is that of the suppression of tall species and the consequent admission of light to the prostrate and low habit species, thus assisting their proliferation.

When treading is continuous a dwarfed habit is imposed upon the species which exist under its influence. When treading is intermittent certain transient therophytes or even the seedlings of perennials may appear upon the bare ground during the abeyance of treading.

Rolling or Compression

The influence of simple compression upon vegetation has several aspects. In the first place tall herbaceus species are injured and suppressed. A prostrate habit is induced upon certain species. The consolidation of the surface soil produces a crust on the soil surface.

To a certain extent the moisture in the upper soil is increased by the fact that particles are brought into closer contact thus increasing capillary attraction. If, however, the soil contains much clay and is moist, a hard crust may be formed, this has a detrimental effect upon moisture conditions.

Very extreme compression such as that produced in an experiment with a ten ton steam roller (29) inflicts severe injury on all gramineous and shallow rooted species as well as those of tall habit. Certain prostrate deep rooted species, e.g. Trifolium repens appear to withstand even this severe injury.

Puddling and Disturbance

This influence is produced by both treading and by the action of the wheels of vehicles. In each case the action is similar as the effect of both treading and of compression by wheels is the same on muddy unstable ground. Puddling and disturbance are produced when the earth is soft and moist, and the foot or wheel, instead of producing their characteristic treading or rolling action, both sink alike into the earth.

It is obvious that the above influences are dependent for action upon a soft wet condition of the earth. Vegetation is crushed and buried or squeezed out upon the surface. It is usually in winter that these actions take place, the earth being hard and stable in summer.

Puddling and disturbance is rarely distributed evenly over an area of ground, such as a gateway or cart track. Some areas are left entirely undisturbed as with the area between the cart ruts and the track of the horses' feet. Other ground is compressed, but not puddled, owing to its harder or drier nature than that of its surrounds, though the compression may be very severe.

Puddling results in great disturbance during winter months with comparative stability during summer. The effect of this is to allow the growth upon puddled areas of therophytes only, which complete their cycle during the period of stability. The severe compression during the stable period allows only the growth of therophytes which are structurally adapted to resist injury.

These are such species as Matricaria suaveolens, Polygonum aviculare, and Senebiera Coronopus.

On the areas which are stable in winter, but where treading is too severe for most gramineous species (excepting perhaps Poa pratensis), certain perennial species exist, e.g. Plantago major and Potentilla anserina. These are unable to withstand puddling in winter, being either buried or squeezed out, though they are adapted to withstand severe compression when the ground is stable.

Seedlings of Plantago major are often abundant upon the puddled areas during the stable period in summer, but they do not survive the winter.

Close Mowing

The effect of close and frequent mowing upon vegetation is quite different to that produced by treading or rolling only, and also to that produced by close grazing.

The effect of close mowing is to defoliate the species down to a point about 1 - 2 cms above ground level. This is carried out without the crushing and bruising influence of the foot and without consolidation of the soil.

It has been seen that frequent mowing reduces leaf size (Section 8) and root range, thus lowering the competitive powers of the species concerned. It is also obvious that tall species are destroyed and prevented from seeding.

The flora produced by frequent mowing as distinct from treading or cutting is one composed of species which possess a low prostrate habit, or are able to adopt such a habit, and thus escape the action of the mower. Such species may be found on any lawn of any standing or on putting greens and similar places, whether they were produced by turfing, seeding down or simply by mowing the original sward.

The following table, taken from a previous publication (30), gives a typical example of the type of herbage produced by continued mowing of an ordinary undergrazed park land.

TABLE XXVII

CRICKET PITCH AND SURROUNDS-HARDWICK PARK

Unmown Portion	%Area Covered	Mown Portion	%Area Covered
Bent (Agrostis spp)	47	Wooly Softgrass (Holcus mollis)	32
Sheeps Fescue. (Festuca ovina)	22	Wild White Clover (Trifolium repens)	12
Tufted Hairgrass. (Aira caespitosa)	6	Heath Bedstraw (Galium saxatile)	20
Cocksfoot. (Dactylis glomerata)	20	Mouse Eared Chickweed (Cerastium spp)	10
Miscellaneous	5	Daisy (Bellis perennis)	13
		Plantain (Plantago spp)	8
		Miscellaneous	5
	100		100

The low prostrate habit of the species on the mown portion in comparison with those of the unmown, needs no elaboration. Not only does close mowing fail to destroy the prostrate species, but by the admission of light greatly encourages their developement. This is a well known phenomenon on lawns and similar places where Trifolium repens, Plantago spp, and Bellis perennis become a serious nuisance.

Protected Areas

The biotic influence in the form of human activity may create areas where there are reverse conditions to those enumerated in the above paragraphs, i.e. areas which are protected from any form of treading, cutting or grazing. A typical example of this is the hedge or an enclosed paddock or steep bank.

In the case of the hedge, the base of the bushes composing it are a protection from any of the above damaging influences. The same conditions exist in the enclosed and unused paddock where all animal influence is excluded or on a steep bank which gives no foothold.

The above areas are usually dominated by such species as Arrhenatherum avenaceum and umbelliferous species such as Anthriscus sylvestris, all of which are unable to withstand any of the mechanical influences of the biotic factor as has been shown in Section 5 .

Engineering Operations

Bare Ground

Bare earth is frequently exposed owing to the baring of the ground by removal of turf, by digging operations or by the deposition of areas of soil of sufficient depth to destroy pre-existing vegetation.

Such areas are characterised by the appearance of therophytes and of species which invade the area by runners, both surface runners and subterranean.

Induced Drought

Engineering operations in the form of excavation frequently produce conditions of drought. This may be found at the top of a bank, at the brink of a channel or in the earth overlying a tunnel or bridge, gravitation being the force which reduces the water content.

The species most typical of these conditions are Holcus lanatus, Holcus mollis, and in the presence of bare earth Hordeum murinum. When the dry conditions exist as a zone, the above species also exhibit zonation.

Conditions of physiological drought may be induced by the formation of impervious hollows where water collects.

*Data regarding the comparative moisture contents of such sites as ends of banks, brinks of channels and footpaths with that of their surrounds are given overleaf.

Deposited Material

Heaps of stone, gravel or sand produce a characteristic vegetation. Cirsium arvense is the most frequent dominant. A stimulus appears to be exerted by the heap upon the deeply buried runners in the underlying or surrounding soil. From investigation the phenomenon is apparently due to freedom from grass competition and its resulting toxic influences.

In the case of the domination of heaps by Agropyrum repens and other species, the comparatively increased moisture content of the soil may exert an influence. Heaps, like sand dunes, contain more moisture than is commonly realised and also provide a cover for the underlying soil, thus increasing the moisture per unit of basal area in comparison with the surrounds.

The deposition of loose material upon the surface of the earth attracts and provides a medium for such species as Urtica dioica, Lamium album, Aegopodium Podagraria, and Mercurialis perennis, all being of practically similar life form.

From a study of the proliferation of Urtica dioica, it has been shown that the deposited material provides shade which prevents premature development of the shoots. The

*The samples were taken in the recognised manner. The analyses were carried out by Mr. E.T. Sykes M.A. at the Field Laboratory. Norfolk Agricultural Station. Sprowston. Norwich.

While the chresard figure is the only one of true ecological significance, total moisture estimation will serve to illustrate the cases in point.

* Soil Moisture Data.

Sites of Hordeum Murinum.

Control (Hordeum absent)		Oven Dry %	Site. (Hordeum present)		Oven Dry %
1. Bank.	(Grimston)	4·32.	No. 1 d. End of Bank.	(do)	1·24
"	(Gaywood)	15·06.	" 2 d. " " "	(do)	3·90
"	(Massingham)	7·24.	" 3 d. " " "	(do)	2·36.
"	(Gaywood)	9·40.	" 4 d. " " "	(do)	4·16.
"	(Grimston)	11·02.	" 5 d. " " "	(do)	8·14.

Sites of Holcus spp.

Control. (Holcus absent)	Oven Dry %	Site. (Holcus present.)		Oven Dry %
Surrounds of Channel. (Gaywood)	12·70.	No. 1. d. Brink of Channel.	(do)	3·58
" " " (Gaywood)	9·38.	" 2. d. " " "	(do)	7·50
" " " (Massingham)	5·34.	" 3 d. " " "	(do)	1·70.
" " " (Massingham)	6·14.	" 4 d. " " "	(do)	2·62
" " " (Massingham)	13·86	" 5 d. " " "	(do)	3·26

Moisture Conditions of Footpaths

Control (Surrounds)	Oven Dry %	Site. (Footpath)		Oven Dry %
Surrounds of Footpath (Gaywood)	9·02.	No. 1. d. Footpath.	(do)	12·52
" " " (Gaywood)	13·30.	" 2. d. "	(do)	9·60
" " " (Massingham)	4·62.	" 3. d. "	(do)	9·44
" " " (Massingham)	3·10.	" 4. d. "	(do)	3·24
" " " (Grimston)	4·72.	" 5. d. "	(do)	6·40.

1 & 2 Clay Soil
3 & 4 Medium Loam
5. Sandy Soil.

* The samples were taken in August 1933 under drought conditions. As some of the samples were apparently air dry at time of sampling, only oven dry estimations were made.

introduction of light to an undeveloped runner of Urtica dioica results in an immediate opening of the terminal bud and a weak chlorotic shoot, this terminates proliferation.

Road side sludge which when deposited cements into a hard heap, usually proves a habitat for Bromus sterilis.

Consolidated surface and the Prostrate Habit

It may be observed that certain gramineous species, and also Plantago spp, Trifolium repens, and Polygonum aviculare assume a more prostrate habit upon a consolidated soil than upon a loose one, and this in the absence of treading.

A possible assumption would be that a constriction of the hypocotyl produces this habit and this would be feasible in rosette plants like Plantago spp. In the case of Polygonum aviculare the long trailing stems are closely adpressed to consolidated ground in contrast to their more bushy habit on loose soil. In this latter case the theory of constriction can hardly apply.

The most probably explanation is that of differing conditions of surface temperature. Under strong sunlight a difference of 10°F has been recorded by the writer upon the actual surface of a loose soil in comparison with a hard adjoining footpath. The hard surface has a higher conductivity than the loose surface, and as heat diffuses away more rapidly it possesses the lower surface temperature. Up to a depth of 5 cms. the soil underlying the hard surface may be 5°F higher in temperature than that of the loose soil.

At night during radiation of heat from the surface, the reverse conditions to the above prevail. The hard surface may be 6°F higher in temperature than the loose.

It is now generally recognised by soil physicists that moisture is not lost so rapidly from a soil with a loose surface, other conditions being equal.

* The whole problem is a complex one, but it would appear that peculiar temperature and moisture conditions are the most likely factors responsible for the prostrate habit.

Induced Illumination or Shading

The erection of a bank running in a E - W direction will produce an illuminated southern aspect on one side and a shaded aspect on the other. Species tolerant of shade may develop upon the shaded side, but on the illuminated side the species are earlier and better developed. There may be a great comparative increase in such species as Trifolium repens and Anthriscus sylvestris.

The planting of a hedge or the erection of a wall gives a shaded habitat on the northern side. On the other hand unless the hedge or wall is placed on a bank there is no increased illumination on the southern side. It is the upward slope of the bank which brings the surface at a right angle to the maximum intensity of the suns rays and thus produces a maximum illumination per unit of area.

In all the above cases increased or decreased warmth of the soil is directly related to increased or decreased illumination.

* Gupta (40) has shown that consolidation of the soil greatly retards flow of moisture and, as transpiration increases, may produce permanent wilting.

Defoliation or crushing of taller vegetation by mechanical means such as mowing or rolling or by the agency of treading or grazing or by the exposure of bare earth leads obviously to greater illumination of the soil surface. This influence results in a marked increase in prostrate species and those of low habit. The effect is most marked upon Trifolium repens.

The Mechanical Influence of Animals

The influence of domestic animals, e.g. horses, cattle sheep and pigs is threefold. In the first place there is treading by the foot, secondly the action of grazing which is comparable to different intensities of mowing, and thirdly there is the selective aspect of grazing, due to the preference of the animal for certain species and a distaste for others.

Treading is more intense in the case of sheep than in other animals owing to their greater activity, and to the small size of the hoof in proportion to their weight. On the other hand sheep frequently graze under drier conditions than other animals and much of the influence of treading is thereby lost.

Horses

The grazing effect of horses is peculiar. Certain areas of the pasture are very closely grazed owing to the close biting habit. Other areas are used for dunging and here the animal does not graze, these areas are also avoided by other classes of stock. On the ungrazed portion tall hemicryptophytes and chamaephytes are dominant. A pasture or paddock which is heavily grazed by horses may be distinguished by the sharp demarcation between the grazed and ungrazed areas. Tables XXVIII, XXIX below give a typical illustration of this condition (see also Figs.138, 139)

TABLE XXVIII

Horse Pasture Terrington Marsh

Grazed Portion	%Area Covered	Ungrazed Portion	%Area Covered
Lolium perenne	30	Dactylis glomerata	40
Poa trivialis	10	Holcus lanatus	25
Poa pratensis	23	Festuca elatior	10
Trifolium repens	20	Phleum pratense	10
Bellis perennis	12	Poa trivialis	8
Miscellaneous	5	Cirsium arvense	7
Total	100	Total	100

TABLE XXIX

Horse Pasture Gaywood

Grazed Portion	%Area Covered	Ungrazed Portion	%Area Covered
Lolium perenne	33	Dactylis glomerata	35
Poa pratensis	21	Holcus lanatus	30
Agrostis spp.	10	Agropyrum repens	10
Trifolium repens	33	Arrhenatherum avenaceum	25
Miscellaneous	3		
Total	100	Total	100

In Figs 138,139, Bellis perennis is very obvious upon the grazed portions, these photographs illustrate fields which have been used as horse pastures for many years. It is noteable in many cases that Cirsium arvense is very abundant upon the ungrazed portion but not on the grazed portion.

On the grazed portions the vegetation is sparse and consists of low or prostrate cryptophytes or hemicrytophytes. The ungrazed portions are dominated by tall hemicryptophytes and phanerophytes which do not tolerate grazing of a severe degree.

Cattle

Cattle do not bite closely but tear the herbage off. The result of this is a longer sward all over the field in comparison with the grazing of horses or sheep.

Cattle dung is dropped in circular patches about 1 ft in diameter. These, if not spread by cultural operations, lead to a bare patch surrounded by a ring of tall herbage. The bare patch, when the dung has decomposed, may become dominated by therophytes or by Rumex spp.

Sheep

Sheep graze very closely and this habit tends to produce a close short herbage very similar in botanical composition to that of a closely mown area. Sheep droppings are spread evenly over the field.

Pigs are characterised by their rooting habit, apart from grazing they expose large areas of bare ground by tearing off the turf. These areas are colonised by therophytes and by runner bearing species, most notably Trifolium repens.

No definite information regarding the effects on the botanical composition of pastures of the separate droppings of the various domestic animals is forthcoming. It is to be observed however that the dung of pigs tends to produce more Trifolium repens than the dung of other animals. This refers to dung applied to the pasture in the absence of the animal, thus eliminating any physical action.

The influence of rabbits is that of very close selective grazing without treading. The foot of the rabbit is light, soft and hairy and cannot exert the influence of a hoof.

The effect of the deposition of earth and sand by burrowing operations is the same as that of the deposition of sand heaps by human agency and is discussed in Sections 6 & 7.

A classical study of the influence of rabbits by close selective grazing upon sandy East Anglian Heaths has been made by Farrow (19). This grazing leads to zonation and partial degeneration of the sward.

Moles

The influence of moles, a non-grazing animal, is simply to deposit heaps of earth. These heaps again exert a similar influence to that of the deposition of sand by human agency. This is discussed in Section 6.

Poultry

Very large areas of semi-natural vegetation are populated by poultry and with the rapid growth of the poultry industry these regions are of considerable though undetermined dimensions.

The influence of poultry upon grassland is peculiarly characteristic. There is a grazing or plucking of the herbage and the intensity of this varies proportionately with the concentration of the head of stock. *Observations upon pens where laying trials are conducted show that with equal number of birds upon equal areas the intensity of grazing varies proportionately with the egg laying capacity of the groups of birds.

The most marked influence of poultry however is the production of coarse tufts of grass, usually Dactylis glomerata, which dominate a pen (Fig.140) This phenomenon

* Norfolk County Council. Laying Trials. Sprowston.

is brought about in the following manner. The scratching of the birds in search of food, and for the purpose of scratching out hollows for "dust baths", eliminates all shallow rooting species and tears out the runners of other species. The only species which survive this activity are the deep rooted and tufted ones of which Dactylis glomerata is most prominent. Lolium perenne sometimes persists and forms tufts as does Arrhenatherum avenaceum and Aira spp. The same tufted condition is produced in Urtica dioica Fig.141.

The influence of young chickens differs greatly from that of adult hens. When the former have been penned the area becomes distinguished by a consocies of Lolium perenne. This phenomenon occurs <u>with unfailing constancy</u> and has been observed both in permanent pastures and upon temporary pastures. In the latter case, temporary pastures consisting largely of Dactylis glomerata have shown pure populations of Lolium perenne where the chickens were penned.

The above phenomenon is apparently due to the fact that young chickens do not scratch or at least not effectively. On the other hand they have a puddling action, especially in the region of the food supply. This puddling influence produces the same result as is observed on a footpath, i.e. the production of Lolium perenne upon the puddled area.

Robinson (41), in a recently published work, describes how ducks, which are heavy puddlers, have converted a grass sward into an associes of Plantago major and "Mayweed" (M. suaveolens) The ducks were removed and the land utilised for hens, resulting in the return to a grass sward.

Robinson also gives definite figures illustrating the direct relation of grazing to egg production.

In a later private communication Robinson reports that Polygonum aviculare has appeared in the duck pens.

Fig.138. Showing field grazed by horses. Note coarse ungrazed patches and heavily grazed patches populated by Bellis perennis. (Tilney St.Lawrence,Norfolk).

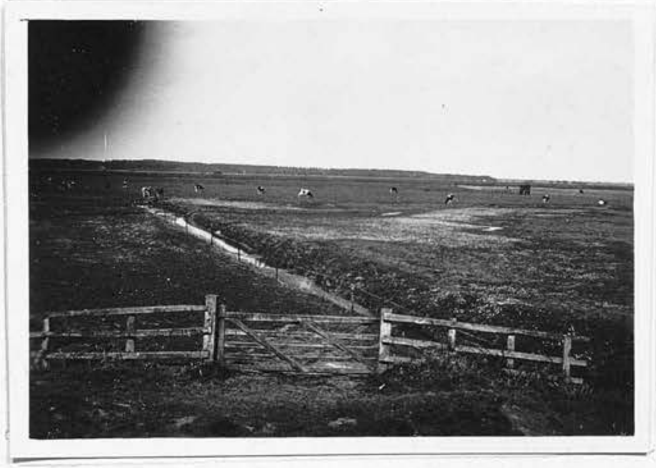

Fig.139. Showing similar phenomenon to fig.139 above. (Wells next Sea,Norfolk).

Fig.140. Poultry pen dominated by Dactylis glomerata. Note coarse tufted habit of the plants. In the right background a separate pen is occupied by young birds,(wire separating pen recently removed) Note absence of tufts of Dactylis glomerata on this area.(Tilney St.Lawrence, Norfolk).

Fig.141. Influence of poultry upon colonies of Urtica dioica. Note bush like habit of the species. (Hilgay.Norfolk).

SECTION

11

THE MECHANICAL IMPROVEMENT OF GRASSLAND

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THE MECHANICAL IMPROVEMENT OF GRASSLAND

In preceding sections of this thesis an attempt has been made to study the mechanical influence of the biotic factor, and its effect upon several types of vegetation. The present section comprises an attempt to apply the findings of these investigations to the improvement of certain classes of grassland, and to point out the economic importance of the studies.

The mechanical improvement of grass land may be described as the method of effecting changes in the herbage, to the advantage of the agriculturist, by means of mechanical agents as distinct though not entirely divorced from chemical agents.

Mechanical improvement may be classed under two headings. Firstly the type which aims at the complete renovation of a pasture which is composed of species of little economic value, which have become overgrown and have formed a mat of root material in the soil surface, resulting in a practically derelict condition. Secondly the practice best described as rejuvenation, or the maintenance in useful order of a pasture in good or fair condition. This latter practice consists of the prevention of the developement of unsatisfactory species and a matted state of the sward by a type of surface cultivation.

There are several types of grassland upon which mechanical improvement has its limitations. In the first place temporary grassland needs little attention in this respect as it is of too short duration to develope condition requiring mechanical interference. Again there are large areas of mountain pasture which respond to mechanical treatment with "re seeding" and manuring, but others are inaccessible to implements or are of so low a rental value as to render the expense of improvement uneconomical.

In the case of very light soils, such as sandy heat or fen, disturbance of the covering of vegetation may result in a serious blowing away of the soil. On light dry soils mechanical action will effect no change in the botanical composition of the herbage, in the same way that on similar soils treading produces no characteristic footpath flora.

Apart from the types enumerated above, there are large tracts of grass land, both pastures, meadows and park land, which require mechanical treatment either with the object of renovation or rejuvenation.

In the case of renovation it is sometimes considered better to avoid mechanical improvement methods, t destroy the pasture completely by ploughing under, and to reseed the ground with the object of producing a new pasture. In some cases this may be the best line of action, but it is not always the case. Often a great expense may be involved, great difficulty may be experienced in establishing a new herbage, and further ploughing of the entire area may be impossible owing to the contour of the land. There are many cases, particularly with park land, where renovation along the lines to be described is indicated.

In the case of rejuvenation by mechanical means the necessity for this practice cannot be denied and the failure to consider its importance has led to the degeneration, or maintenance at a low economic level, of much of the grass land of this country.

It has been claimed and is certainly true that renovation and rejuvenation may be effected by close compounding and controlled grazing with livestock, instead of by the use of implements. On the other hand the use of livestock for this purpose is rarely either practicable or economic from the agriculturists point of view.

<u>The Renovation of Matted Pasture</u>

Large areas of the country are composed of pasture land which is in a matted condition. The condition is not common upon a limestone or chalk soil, but occurs chiefly upon sandy or clay soils. This type of grassland is most common in the North of England and the industrial Midlands, especially where a pall of smoke exists.

<u>The Nature of Mat</u>

The dominant species of a matted pasture are Agrostis spp, Festuca spp, and Holcus spp. Nardus stricta and Aira spp do not form mat in the true sense of the word, they possess deep thick roots with few superficial secondaries and what appears to be mat is really a dense mass of basal leaf sheath.

The three mat forming species mentioned above are all possessed of a surface rooting habit, and this habit is stimulated by undergrazing. It has been shewn that close cutting, treading and grazing restrict root developement (21) conversely undergrazing allows excessive developement of surface root. Undergrazing may be due to understocking, to unrestricted range, to unpalatability of the herbage owing frequently to smoke pollution. Localised undergrazing may occur as a result of selective grazing, i.e. the neglect of colonies of certain species owing to a preference for others.

Mat may vary in thickness from 1 cm to 15 cms. The top layer is loose and frequently contains moss, while the lower layers may have decomposed to a peaty material, and there is never any sharp demarcation between the lower layers of the mat and the soil. The exact proportion of its components cannot be determined, but it is largely root fibre.

The influences of mat upon the habitat and its component species may be enumerated as follows:

(1) Mat is highly absorbant and retains moisture at the surface of the soil, until evaporation takes place.

An experiment by the writer showed that five samples of Agrostis-festuca mat, totalling about 1250 c.c. in volume, and of total weight 1121.75.Grms (air dry), absorbed when exposed to heavy rain overnight, and again when soaked in water, after drying, approximately 1150.0 gms of water. Only an approximate estimate was possible owing to continued dripping.

It will be seen that the heaviest rainfall may be prevented from reaching the soil by a thick mat. It may be observed that on matted pastures the soil is dry beneath the mat, even where water is lying on the surface of the ground.

An experiment was conducted in the following manner:- Samples of soil were taken to a depth of 20 cms from bare patches where matted turf had been removed for lawn making. (Hardwick Park, Derbyshire 1929) These patches had been exposed to winter rain for some months.

A further set of samples were taken from beneath the matted turf in patches adjacent to the above. The turf was cut away to the same depth as in the case of the exposed patches described above, and the soil was sampled immediately to a depth of 20 cms.

A moisture estimation was made by air drying and the following results were obtained:-

Soil exposed several months....... 19.3% moisture

Soil from beneath mat............ 6.8% "

The above observations and figures are also borne out by the characteristic xerophytic species which dominate most matted pastures, e.g. Agrostis spp, Festuca ovina, Holcus mollis, Luzula spp.

(2) Owing to moisture conditions set up by the mat, only surface rooting species on the one hand and very deep rooted species on the other hand can exist. The former, such as Agrostis spp, Festuca ovina, Holcus mollis and Luzula absorb surface water while the latter species such as Nardus stricta, Aira caespitosa and occasionally Trifolium repens can penetrate to great depths. (See Bisect 1.)

(3) An acid condition is present owing to accumulation of peaty material and the exudation of CO_2 from living roots.

(4) Fertilisers in the form of chemical manures and lime, also the droppings and urine of animals are prevented from reaching the soil.

On meadow land where a portion of the field was disc harrowed and the whole field top dressed with dung, the disc harrowed portion was sharply demarcated from the other by the fact that it was a deeper green in colour and yielded about 25% more grass per hay. This experiment was carried out at Ashgate, Derbyshire, 1928. (11,

(5) During severe frosts the chamaephytic species of a badly matted pasture are killed off, while deep rooted cryptophytes and hemicryptophytes persist. This was very noteable during the "great cold" of 1929.

The undesirability of a matted condition in a pasture is obvious from the above observations.

<u>Eradication of Mat</u>

Experiments were carried out in Hardwick Park, Derbyshire by the writer, in collaboration with Capt. J.D. Penrose agent to His Grace the Duke of Devonshire, the owner of the Park (31). The first attempts were made in the winter of 1926-27, on a badly matted area of about 50 acres in extent. Up to that time there was a popular belief that mechanical interference with a permanent pasture was harmful. A few agriculturists had, however, observed beneficial results from close compounding of livestock, and one at least had practiced heavy harrowing.

In 1926 the beneficial influence of cutting a pasture in two directions with a disc harrow in increasing the population of Trifolium repens was noted by Hunter (32).

No definite attempt had been made to assess the effect of mechanical treatment, must less to study its influences in detail.

The first process, carried out on 20 acres, was to harrow out the mat with ordinary iron harrows drawn by a tractor and weighed down. This was really a combing effect and enormous quantities of mat were gathered up and burnt.

Prior to treatment the herbage consisted of Agrostis stolonifera, Festuca ovina, Holcus spp, a small proportion of Aira caespitosa in scattered colonies, and an evenly distributed proportion (about 1%) of Trifolium repens.

The result of the treatment was an increase in Trifolium repens to about 10%. Formerly suppressed species such as Lolium perenne, Poa pratensis and Bellis perennis began to multiply.

As regards the habitat itself, surface water disappeared and the soil presented a moist well drained appearance. Livestock shewed a marked preference for the area and it was heavily grazed, thus a steady improvement set in.

In spite of the benefits of the above treatment, it was noted that the changes in the herbage were not so revolutionary as those resulting from the formation of a footpath upon a coarse matted pasture or from the close compounding of livestock.

In view of the above observation a further attempt was made choosing a line of treatment which aimed at the imitation of the action of the foot or hoof in wet weather. (This experiment and its result are already described in Section 3, but are repeated here for convenience.)

The turf was cut frequently in two directions by a disc harrow on a very wet day, until the soil was worked into a morass. It was then heavily rolled.

The weather during the succeeding weeks (March and April 1928) was warm and moist and a covering of herbage established itself in remarkably short time. The change was a very remarkable one and an independant analysis was carried out by Mr.A.Roebuck of the Midland Agricultural and Dairy College. The results were as follows:-

Untreated Portion

		Per cent
	Agrostis spp	35.4
	Cynosurus cristatus	24.6
	Festuca ovina	23.1
	Luzula spp	9.2
Miscellaneous	Lolium perenne, Trifolium repens, Ranunculus spp, Holcus lanatus, Moss	7.7
		100.0

Treated Portion

	Poa pratensis.	50.9
	Cynosurus cristatus	21.7
	Agrostis spp.	9.1.
	Lolium perenne	1.0
	Trifolium repens	12.0
Miscellaneous	Holcus lanatus, Festuca ovina, Ranunculus spp	5.3
		100.0

The change is so closely similar to that produced on a footpath (except that no zonation occurred) that it is plainly indicated that the same influences were at work. Much of the Poa pratensis, however, must have arisen from dormant seed as in the case of the experiment on the influence of treading (Section 3 page 64).

Apart from the changes produced in the herbage there was a gradual disappearance of the mat by decay in the soil.

Further experiments conducted in the same way, but in dry weather, did not result in the same radical changes. Recovery was slow and Trifolium repens increased, but Agrostis, Festuca and Holcus spp still persisted and there was no increase in Lolium perenne or Poa trivialis.

It is obvious that renovation of pasture by eradication of mat must consist of a severe cutting of the mat and mixing with the soil during wet weather. This must be followed by a heavy rolling to press the soil together and prevent drought and frost affecting the species present. The work should be done before February to avoid risk of a dry spring.

A trial of various types of implements for the above work was conducted at Hardwick Park in November 1928. The following implements were tested:-

Description of Implements	Effect upon Turf
Tractor cultivator	Deep laceration at wide distances.
Rotor Tiller	Complete pulverisation.
Spike Roller	Pieces of earth thrown up. Worm cast effect.
Disc Roller	Incision and compression.
Disc harrow	Laceration and partial invertion.
Pitch pole harrow	Close and thorough laceration.
Rejuvenator	Close and shallow incision.

The best results were obtained from the Disc harrow and also from the Pitch pole harrow. Both implements were followed by a roller.

In many cases renovation can be augmented and hastened by the application of fertiliser, and seeding with Trifolium repens, Lolium perenne and Poa spp.

Rejuvenation of Pasture

This practice aims at producing a new flora similar to that of the footpath by the method of destroying by bruising Agrostis spp, Festuca spp, Holcus spp, etc., and the consequent removal of their competition with Trifolium repens, Lolium perenne, Poa spp, Dactylis glomerata, etc. Attempts up to the present have been in the nature of shallow cutting.

Trials were made by the writer, with many types of implements, aiming at an imitation of the influences acting upon the footpath. No success was recorded for any harrowing or tearing device which pulled out the species without descrimination between life forms. Rollers or wooden devices aiming at a crushing effect were ineffectual and scraping devices of steel or wood slid over the surface.

In July 1932, the suitability of rubber as a material likely to produce the desired effect, came to the writer's notice.

Experiments were made with a hand squeege upon a mixed herbage under wet conditions.

Quadrats treated in this way were kept under observation. The heavy rubbing tended to kill out the species Agrostis, Festuca, and Holcus, leaving the buds of Lolium perenne, Poa pratensis and Plantago spp in a living condition below the soil surface. The runners of Trifolium repens were left in a living condition (see Sec. 3 pages 68-9)

Rejuvenator Utilising Rubber

An implement has been designed by the writer (and provisionally patented) a full description of which is appended overleaf.

Five of these implements are now in use in the County of Norfolk, and one in Breconshire.

The first one was tried out in February of the present year (1933). *The immediate result was a lethal effect upon most of the colonies of Holcus spp. and Agrostis spp. The Lolium perenne, Poa pratensis and Trifolium repens survived the treatment and within six weeks there was a marked increase in the amount of Lolium perenne followed by a more profuse growth of T. repens.

Unfortunately a severe drought made detailed analysis impossible.

Conclusions

Mechanical improvement of grassland is defined in this work under two categories. Firstly the reclamation or "renovation" process, which aims at the elimination of mat and the consequent removal of all its harmful influences. This is effected by mechanical means.

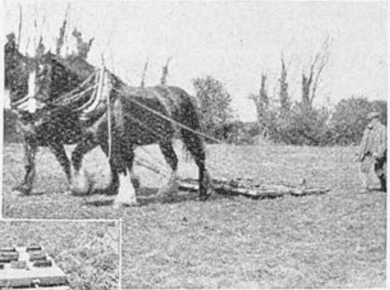
Secondly there is a process distinguished in this section by the term "rejuvenation". This should be practiced upon land not requiring drastic mechanical "renovation", or upon land which has just received this renovation treatment.

While "renovation" effects necessary and beneficial changes in the habitat by eliminating matted conditions, it does not produce the radical changes in the flora as observed on a footpath. "Rejuvenation" aims at producing the latter effect by a surface action which bruises and destroys the undesirable species allowing the desirable ones to survive by virtue of their peculiar life form.

* See Figs 23. A & B. Section 3.

" The Bulletin of the Rubber Growers Assn."
Vol 15 No 7. July 1933.

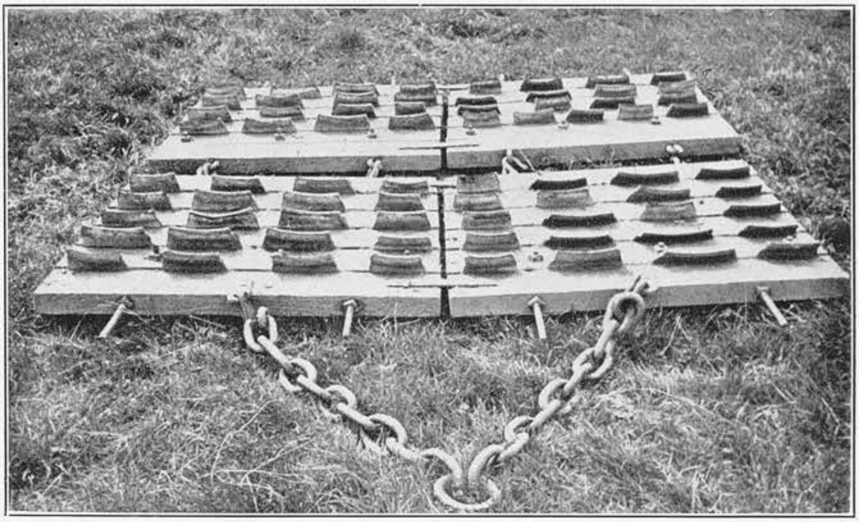
An ingenious device has recently been invented for rejuvenating grassland. It is found that a footpath is dominated by the best grasses and clovers and it has been shown that this is due to the action of treading and puddling in wet weather. To reproduce as near as possible the action of the feet, the inventor of the device uses sections of



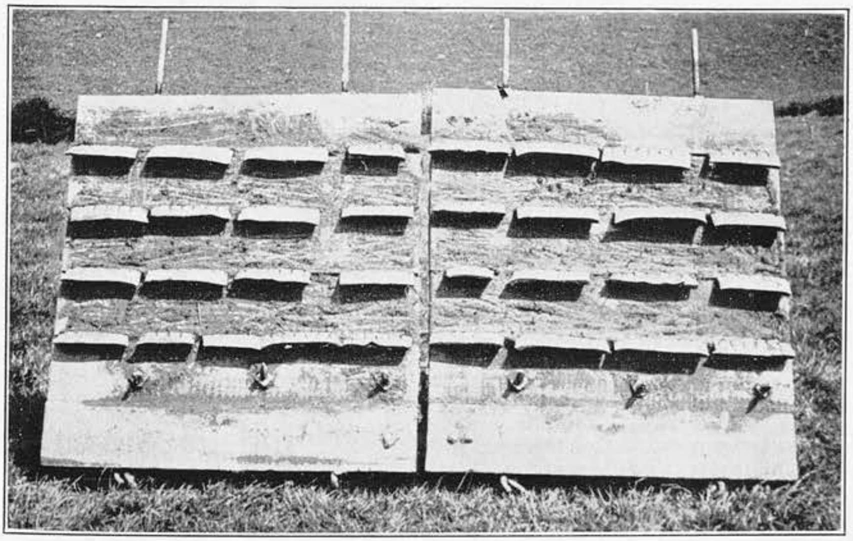
old tyres clamped in rows between wooden boards, resembling a battery of squeegees. The rubber gives rigidity but sufficient elasticity to bend back and liberate dead grass. The rejuvenator is operated when the ground is wet.

A NEW TYPE OF GRASSLAND REJUVENATOR.

A NEW type of grassland rejuvenator has been invented and provisionally patented by Mr. G. H. Bates, of the Department of Agricultural Education, Norfolk County Council, Norwich. The object of it is to put into effect upon a pasture the forces which in nature produce the characteristic flora of a footpath.



Bates' Grassland Rejuvenator—Upper Surface.



Underside of Rear Sections.

It is generally known that a footpath is dominated by the best grasses and clovers, however poor the remainder of the pasture may be. It has been shown that this phenomenon is due to the action of treading and puddling in wet weather, which results in the death of undesirable species and the survival of others.

The chief feature of the implement is the utilisation of rubber as the active agent, as this possesses a gripping action not exhibited by metal. In the implement shown in our illustrations the rubber was obtained from discarded motor tyres. The tyre is cut across sectionally into pieces from 6 in. to 12 in. long at the outer circumference, according to the size of piece required. Each section is then cut longitudinally down the centre of the tread into two halves.

The body of the implement consists of four sections, each composed of deal boards, 3 ft. by 6 in. by 2 in. The boards are braced together by two iron rods running through them, and are tightened by a nut and bolt at the end of each rod. The front sections are connected to the rear sections by "S" hooks, and the two front sections are kept apart during draft by a metal plate. The two front sections each possess three 2 in. long tines, alternating with four tines in each of the rear sections.

The pieces of rubber are clamped in rows between the boards, and resemble batteries of squeegees. The active part of the rubber is inclined forward, and the cut edge of the tread scrapes the ground. The conformation of the tyre gives rigidity, but sufficient elasticity to bend back and liberate dead grass and mud, and this prevents choking. Only about 2 in. of the rubber projects from the lower surface of the section.

The implement is suitably weighted to prevent bouncing and give the most effect. It can, when fully weighted, be drawn by two horses. The drawbar or chain is long and inclined upwards to prevent lifting. The implement will take a 6-ft. breadth, but can be made wider for tractor work. It must be operated when the ground is wet.

Apart from the rejuvenating action, the device will spread dung and molehills, and generally level and compress the surface. It should prove useful on golf courses when used without the tines.

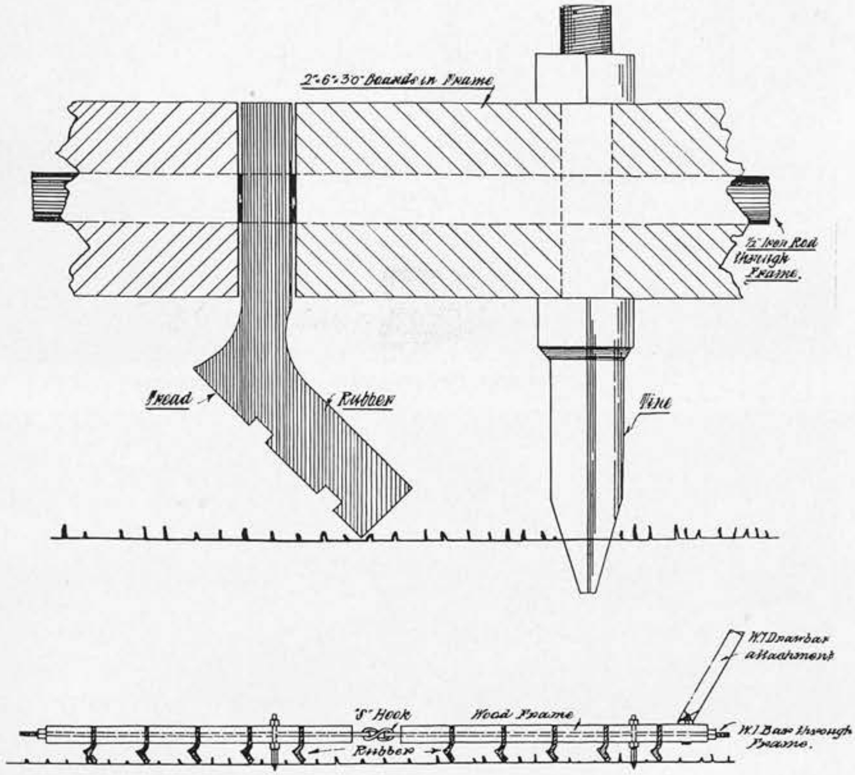
Trials of the rejuvenator have been carried out in Norfolk, and after only six weeks a marked improvement of the herbage on treated areas, in comparison with untreated, was to be seen. After treating 100 acres, the rubber exhibited no sign of wear.

The implement will be included in an educational exhibit by the Department of Agricultural Education of the Norfolk County Council at the Royal Norfolk Show, King's Lynn, on June 21 and 22.

A LAND TYRE DEMONSTRATION.

THIRTY-SEVEN members of the Oxfordshire County Branch of the National Farmers' Union, accompanied by a small party of farmers from Northamptonshire, witnessed a recent demonstration of the Dunlop land tyre at Ashold farm, Warwickshire.

A horse was attached to an iron-tyred cart weighing 10 cwts., and having a load of 9 cwts., but the cart was stalled on the test incline. On the other hand, on two occasions that the horse was attached to a pneumatic-tyred cart weighing 7 cwts., it negotiated the hill without any difficulty, although in one instance the load was 18 cwt. and in the other 27. The visitors also inspected the rubber flooring in the cowshed.



Bates' Grassland Rejuvenator—Sections.

Contracts have been signed for the growing of sugar beet for the second Anglo-Scottish factory at Cupar to the extent of upwards of 2,000 acres.

Farmers and others are invited to pay a visit to the Rothamsted Experimental Station at any convenient time from now until the end of October to see, among other things, how modern fertiliser and cultivation problems are being investigated. Experiments dealing with bare fallowing and rotary cultivation are in progress and good types of implements are on view.

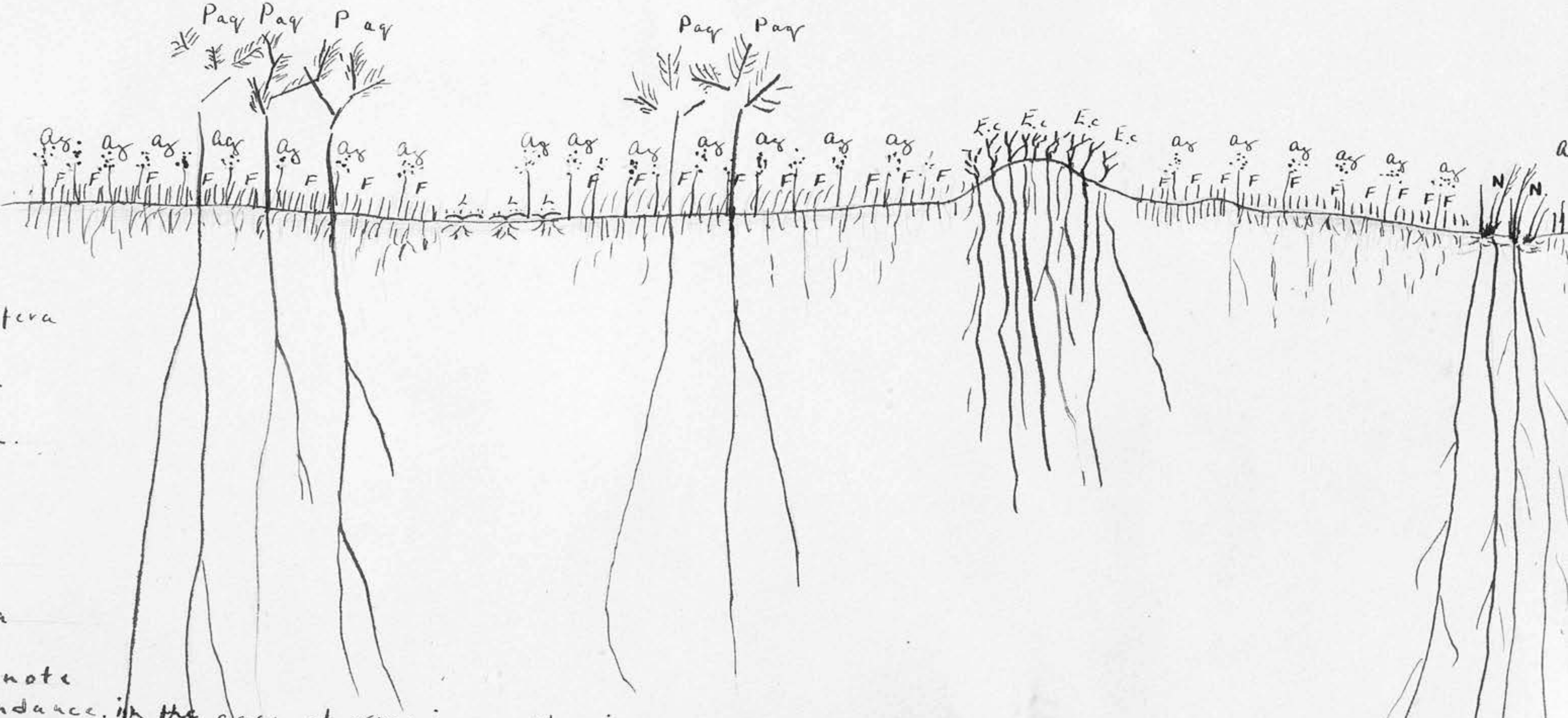
THE 1934 ROYAL SHOW.

THE preliminary work in connection with the holding of the Royal Show at Ipswich in 1934 has already begun well, and an inaugural meeting recently held at Ipswich was most certainly full of promise, for, we understand, it was one of the most enthusiastic of its type for a long period of years.

The Show will be held from July 3 to 7, and the Earl of Stradbroke, who was Parliamentary Secretary to the Ministry of Agriculture in 1928-29, has been invited to become president of the Society for that year, and his election will be proposed at the annual general meeting of members to be held in December. The choice of the Earl of Stradbroke for the office is regarded as a very judicious one, for he is an influential agriculturist in East Anglia.

It is claimed that the implement described above is the only one in existence which effects this influence, and that it shews every promise of success.

Bisect. 1. Massingham Heath (Norfolk)



Symbols.

ag. Agrostis stolonifera

E.c. Erica cinerea

F Festuca ovina.

L Luzula. spp.

N Nardus stricta

P aq Pteris aquilina

Symbols do not denote abundance in the case of gramineous species.

Showing extreme types of root systems (deep and shall

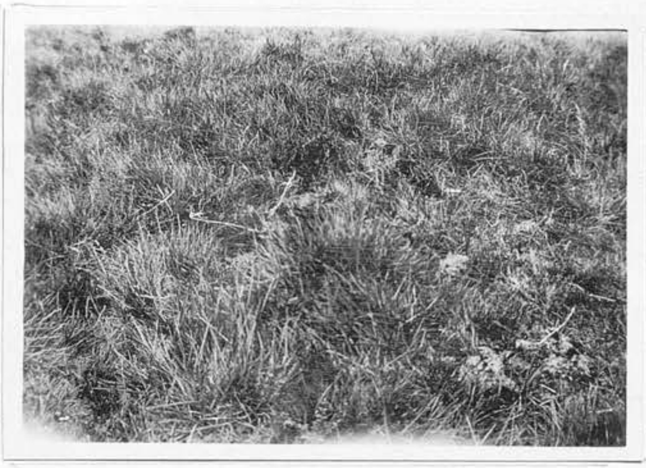


Fig.142. Grassland consisting of Agrostis spp,Festuca ovina spp. Aira caespitosa and possessing a dense surface mat of root material. Prior to mechanical treatment. (Hardwick Park, Derbyshire)

Fig.143. Showing surface of ground (shown in Fig.14 abov after mechanical treatment by lacerating the tu and puddling by a heavy rolling in wet weather. (Note tractor wheel marks)

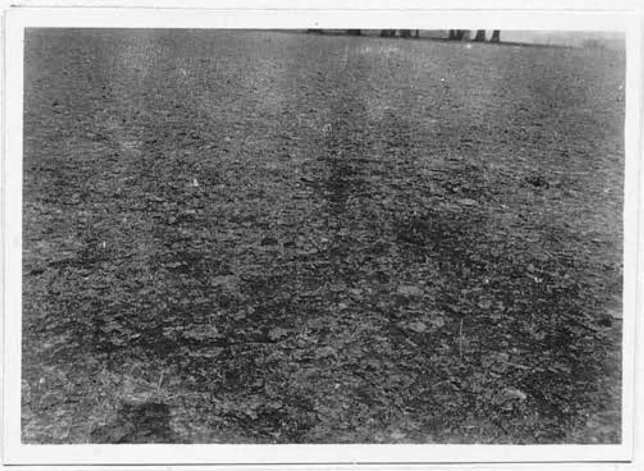


Fig.144. Extended view of ground shown in Fig.above.

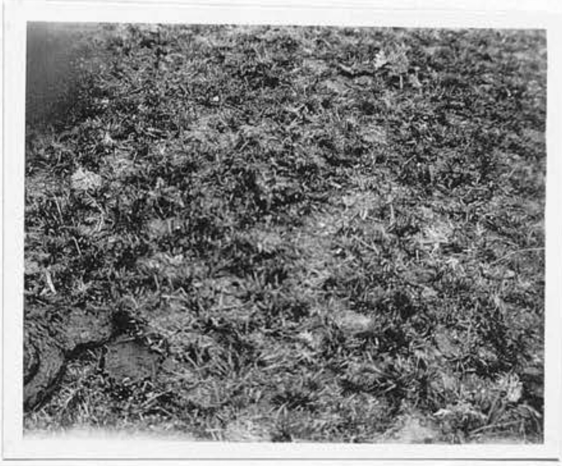


Fig.145. Showing recovery of the vegetation after mechanical treatment. (Same area as shown in figs.142 — 144 above.

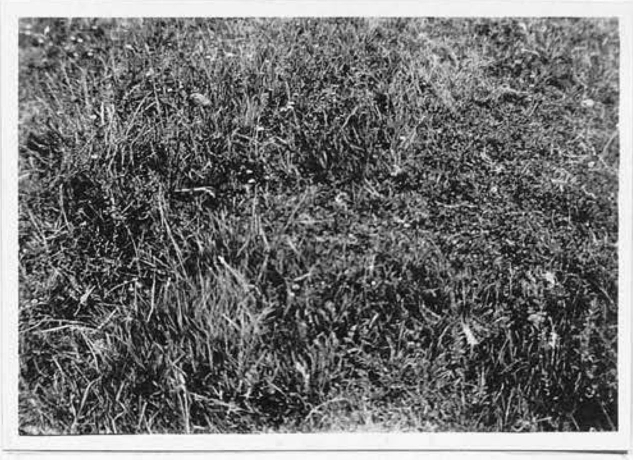


Fig.146. Showing complete covering, by "new" vegetation, of the area shown in Figs.142.143&145. above. In the top left corner of illustration a colony of Trifolium repens is visible, marked by flower heads. A large colony of Trifolium repens is seen at the right of the illustration, marked by several small flower heads. A few flower heads of Bellis perennis are seen at the top middle line of the illustration. Note that the coarse tuft at bottom left corner of fig.142 is still visible in the above, not having been completely destroyed.

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